# Dental Occlusal Form and Function in *Equus capensis*:

## Evaluating a Controvertible Taxonomic Status

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**Megan Malherbe**

Supervised by Dr. Deano Stynder and Prof. Rebecca Ackermann


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**Department of Archaeology**

**University of Cape Town**

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# Abstract

The Giant Cape zebra *Equus capensis* is one of the most iconic fossil herbivore species of the South African Quaternary. It is widely believed to have persisted relatively unchanged in its morphology for the duration of its existence, that encompassed the mid-to late Pleistocene. Described as a large-bodied equid, its skeletal remains were originally regarded as distinct and readily distinguishable from those of other fossil equids, especially with respect to their large size. This applied particularly to its cheek teeth, that were described as large with unique occlusal enamel morphology. Palaeontologists have generally accepted the taxonomic status of *E. capensis* without question. However in reality, its taxonomic status is far from incontrovertible as many of its definitive morphological traits are based on conjecture.

*Equus capensis* was originally described on the basis of a large mandible embedded in limestone that had much of its dental row obscured. The rest of it was reconstructed using unassociated, usually isolated osteological elements from a variety of localities. Perhaps not surprisingly, apart from size, researchers have struggled over the years to distinguish between *E. capensis* skeletal elements and those of other fossil equids. An ancient DNA study of four *E. capensis* teeth further compounded the uncertainty around its taxonomic status by exposing a high degree of genetic similarity to *E. quagga*.

The present study represents the first systematic investigation of morphological traits originally used to define *E. capensis*. Specifically, it considers dental occlusal enamel form and function to

help shed light on the taxonomic status of *E. capensis*. Geometric morphometrics was used to compare premolar and molar occlusal enamel pattern in *E. capensis* and a large comparative equid sample. This was followed by an evaluation of levels of enamel complexity. Next, traditional linear methods were used to compare overall occlusal dental form. Finally, mesowear analysis was used to evaluate dental function. Analyses of dental occlusal enamel form were able to distinguish *E. capensis* teeth from those of equids in the comparative sample on the basis of size, but not shape. This result is telling since the shape of dental occlusal enamel bands carries greater taxonomic significance than their size. Size is easily influenced by environmental factors and may fluctuate through time. Also, analyses of mesowear patterns were unable to separate *E. capensis* teeth from those of *E. quagga*, with which it is thought to have co-occurred. Overall the results of this study do not support the legitimacy of *E. capensis* as a taxon and lays the ground for additional enquiries.

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# Chapter One

## Introduction

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### 1.1 Uncertainty Around the Taxonomic Status of *Equus capensis*

*Equus capensis* is purported to have been a large-bodied zebra that existed mainly in South Africa during the mid-to late Pleistocene. Its appearance in faunal lists from a wide variety of archaeological and palaeontological sites suggests that not only was it a long lived, but also a wide-ranging species, that was able to adapt to a variety of ecological contexts. Over the years, its validity was never really questioned, and neither were the characteristics used to identify it. It was generally accepted that its teeth were easily distinguishable from those of other fossil equids on the basis of their large size, but more particularly, their unique occlusal enamel morphology. However, many faunal analysts have struggled to consistently separate out *E. capensis* teeth from other equid teeth in faunal assemblages using occlusal enamel morphology and have instead relied only on large size.

*Equus capensis* was originally described by Broom (1909) on the basis of a left mandible, found embedded in a limestone slab that had washed up on a beach at Yzerplaats, Table Bay, in 1907. In his description, Broom (1909, 1913) noted that its large size was suggestive of a domestic horse, but because it was entombed in limestone, it was more likely derived from an extinct equid. A significant portion of its dental row was covered by limestone, which meant that Broom (1909) had to infer its dental occlusal enamel pattern. At the time no maxillary teeth had been found, but in subsequent years *E. capensis*' upper dental enamel pattern was also described from a few

isolated teeth that Broom (1909, 1913) assumed belonged to this large equid. Following on from Broom's (1909) initial characterization of *E. capensis*, various other scientists through the years have provided their own interpretations of its dental enamel morphology (Cooke 1950, Churcher and Richardson 1978, Churcher 2000). As a result, there is currently a great deal of incongruity on the specificities of enamel features that are assigned to *E. capensis*. This might explain why researchers have struggled to use dental occlusal enamel morphology to identify *E. capensis* teeth. However, an ancient DNA (aDNA) analysis of four fossil teeth have raised another possibility, namely that *E. capensis* was not a unique species, but was an extinct morphotype of the plains zebra *Equus quagga* (Orlando *et al*. 2009).

Despite its identification more than a century ago, there has never been a quantitative investigation of the morphological traits that have been used to define *E. capensis*. All studies have been qualitative, descriptive and have not been based on systematic comparisons with other equid taxa. This, in conjunction with the results of the aDNA study, has led to some doubts around the taxonomic status of *E. capensis*. The current study is the first to systematically examine the dental occlusal enamel patterns of specimens assigned to *E. capensis*. Material from 19 Pleistocene localities located across South Africa were analysed and compared to a variety of fossil and extant equids using an array of quantitative methods. This study also places special emphasis on comparing *E. capensis* to *E. quagga* given the abovementioned aDNA evidence and questions around the relationship between these two taxa.

### 1.2. Thesis Outline

The remainder of this dissertation is laid out as follows:

Chapter Two provides an overview of the literature surrounding the topic as a whole, summarizing previous research. The 55-million-year history of equid evolution is explored, and its associated complications in taxonomy. A summary of the historical classifications for *Equus capensis* is discussed, and how the equid has been analysed in previous research. The context of the mid-to late Pleistocene is investigated, detailing the time period from which *E. capensis* is recorded. The climatic oscillations prevalent at the time are discussed, as well as subsequent animal responses. The depositional contexts of the studied *Equus* material are also considered, particularly with regards to issues of stratigraphic integrity and accurately reconstructing chronometric data. Lastly, the use of dental morphology and morphometric approaches for investigating the taxonomic distinctiveness of *E. capensis* is explored.

Chapter Three provides details of data collection localities, number of specimens per species, and which specimens were used for each analysis. The chapter then outlines the four analytical methods used (2D geometric morphometrics (relative warps thin-plate splines), traditional linear measurements, occlusal enamel complexity and mesowear) and the reasons for their employment.

Chapter Four presents the results of the analyses. Each analysis is presented separately, and emphasis is placed on the most relevant of the results.

Chapter Five evaluates the results of this study in conjunction with the historical knowledge. Issues in the naming of *E. capensis* are explored, as well as what the findings of this research (in combination with aDNA discoveries) may suggest. The effects of climatic fluctuations on changes

in body size during the Pleistocene are discussed, specifically in relation to equid species in Africa. Lastly, the main conclusions of the research are summarized, potential limitations highlighted, and suggestions are made for possible future research avenues.

# Chapter Two

## Background

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### 2.1 Equid Evolution

#### 2.1.1 A Complex 55-Million-Year History

The evolution of Equidae is often held forth as a prime example of the process of natural selection and environmental adaptation (Beasley 1903, Simpson 1951, Eisenmann 2004, Mihlbachler *et al.* 2011, Evans and Janis 2014, Orlando 2015). Early on (Marsh 1874, Cope 1887), equid evolution was claimed to have been teleological and linearly progressive, leading to the equids that we know today as the final product, with all of the other extinct variants being diversions of sorts (Woodburne and MacFadden 1982, MacFadden 2005a). For long, this 'direct progression' hypothesis was accepted; *Equus* was considered the only equid genus to have survived so many years of evolution and transition from a common beginning in the genus *Hyracotherium* roughly 50 million years ago (Ma) (Kefena *et al.* 2012). However, we now know that the evolution of Equidae was far more complex, with a branching and complex phylogenetic tree (MacFadden 1986, Gould 2002, Eisenmann 2004), where the various species that we know today are in fact merely the indiscriminately surviving side branches. Although the 55-million-year history of their evolution is now comparatively clear and well represented in the fossil record (Simpson 1951, Groves and Ryder 2000, MacFadden 2005a, Orlando 2015), the details of this evolution are still being fleshed out. Sequences of particular acquisitions (such as increase in body size) and various adaptations (brachydont to hypsodont teeth) are complex and divergent, with numerous transformations (Woodburne and MacFadden 1982, Simpson 1951, Evans and Janis 2014). The

constant new information that is being brought forward in the form of fossils and DNA evidence on extant and extinct species, has meant that conventional thoughts on equid evolution have changed, with phylogenies becoming bushier than ever (Eisenmann 2004).

While the evolutionary history of equids is an extensively explored and well covered topic, there are still many areas that perplex scientists and many questions that are still to be answered. The sheer volume of variation amongst genera and species makes it extremely difficult to accurately trace the evolution of equids (Eisenmann 2004). Added to this, while it is known that anatomical features will naturally transform, it is not always true that these transformed features equate to evolved features. The result of this fact led to much speculation regarding the overall evolutionary trajectory of these mammals, where conclusive taxonomy has yet to be achieved, nor has an agreement on the chronological order of speciation events (Oakenfull *et al.* 2000).

An apt analogy for the complex evolutionary path of horses is that of "lateral stepping" (Gould 2002: 93) rather than a constant progression. The pathways are indirect, and each step consists of numerous options with no central direction, hence the uncertainty on phylogenetic details. Furthermore, the changes that took place over so many millions of years, from *Hyracotherium* to the sole-surviving *Equus*, represent an unquestionably long-term and convolutely large-scale evolutionary process (Hunt 1995). The fact that these genera are fundamentally nothing alike (Fig. 2.1.1) illustrates this truth. Interestingly, the evolutionary trajectory that began with *Hyracotherium* only started to diversify during the latter stages of equid evolution (Fig. 2.1.2), with more than the first half of their evolutionary history occurring with very few branches (Groves and Ryder 2000).

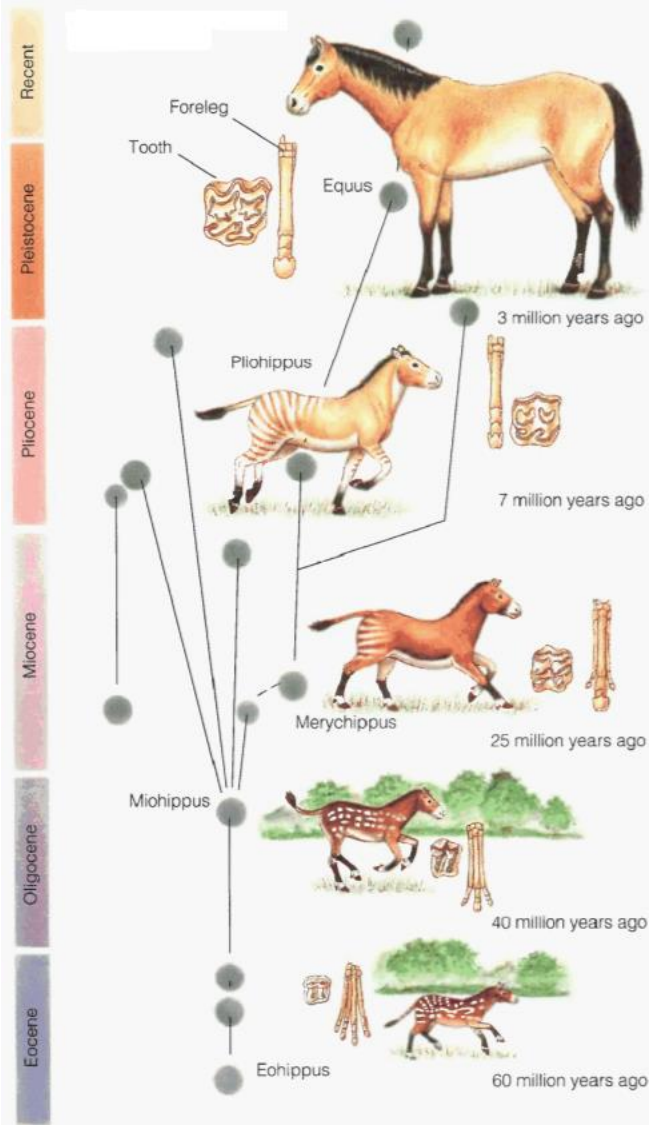



**Figure 2.1.1** Evolutionary changes from forest dwelling *Eohippus* at 50 Ma to modern day grazing *Equus* (Chiras 1999). The grey circles indicate the various species that arose from a common ancestor – the diagram (not a cladogram) makes apparent that the evolution of the modern horse was not linearly progressive.

The earliest known and recognised ancestor in the comprehensive equid family is the aforementioned *Hyracotherium* from the Eocene; a small dog-like mammal with four toes on the forefoot and three toes on the hind foot (Beasley 1903, MacFadden 2005a, Kefena *et al*. 2012, Orlando 2015). The earliest fossil equid forms were found in North America and it has since

become widely accepted that this is where equids originated (Orlando 2015). These mammals had brachydont molars with sheering crests that were poorly developed (Groves and Ryder 2000, Mihlbachler *et al.* 2011, Kefena *et al.* 2012). The teeth were seemingly the first feature to evolve, with *Orohippus* (the transitional form between *Hyracotherium* and *Epihippus*) looking much like Hyracotheres in all aspects apart from their teeth. In addition to more pronounced shearing crests, the last premolar in *Orohippus* became molariformed, providing it with an additional grinding tooth (Hunt 1995). *Epihippus*, which existed during the mid-to late Eocene, was also similar morphologically to *Orohippus* and *Hyracotherium*, but developed a larger central toe on each foot, as well as the molarization of the last two premolars, resulting in five grinding cheek teeth (Beasley 1903, Hunt 1995). *Mesohippus*, which existed during the latest Eocene and Oligocene, became the first three-toed horse (Groves and Ryder 2000) that was also not dog-like, with a longer neck and face, an equine brain and a taller stature. Added to these feature developments, the last three premolars were now molarised, resulting in *Mesohippus* having six grinding teeth, similar to extant equids (Hunt 1995). The horse family began to split into three distinct evolutionary branches during the Early Miocene, namely (1) three-toed browsers (*Anchitherium*), (2) pygmy horses (*Archaeohippus*) and (3) the ancestors of the genus *Equus* that underwent a browser to grazer transition in response to the appearance of grasslands (*Parahippus*) (Hunt 1995). The effects of climatic changes on speciation are arguably most evident in the evolutionary processes of the equid lineage.

### 2.1.2 Major Trends in Equid Dental Evolution

Equid morphology has changed substantially over 55 million years, largely in response to the aridification of global environments. The earliest equids evolved in closed environments, such as

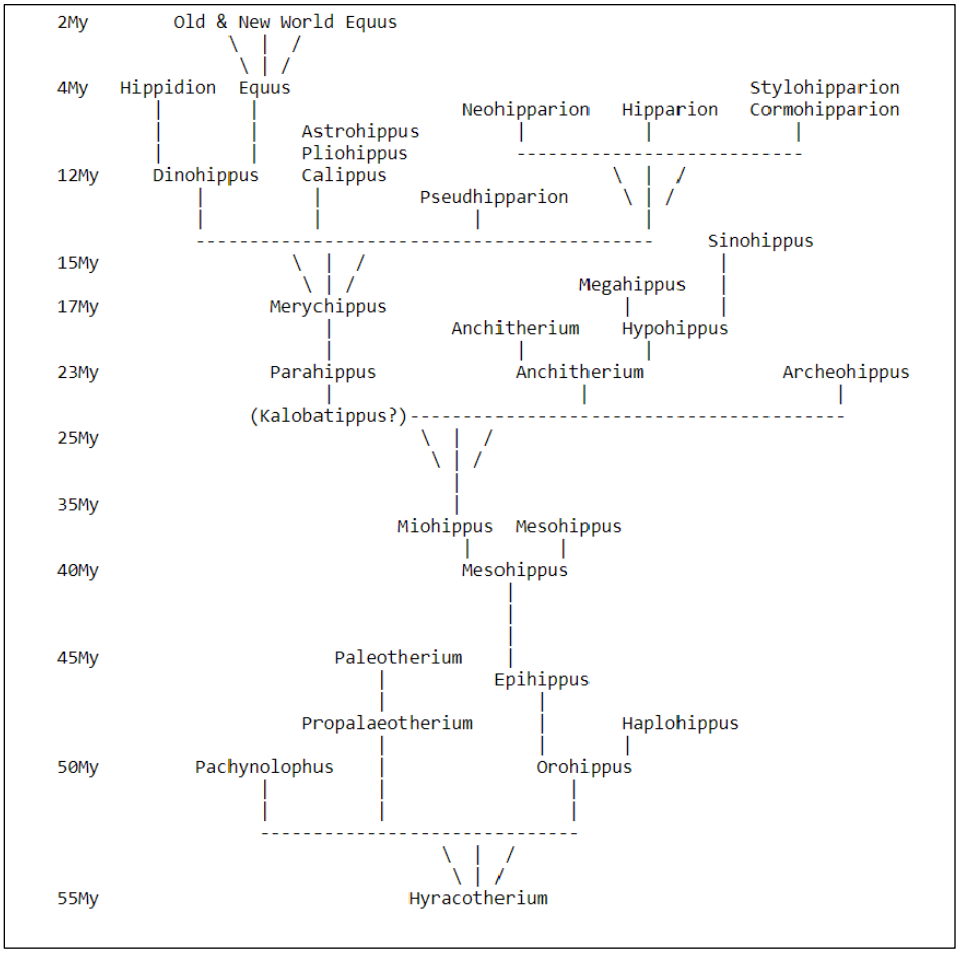



**Figure 2.1.2** Equid family tree (Hunt 1995). The timescale is compressed (the Oligocene is condensed almost to nothing) to prevent the tree from being too long. All names on the tree are entire genera, so each genus represented includes a collection of closely related species.

forests and woodlands, which dominated the globe during the Eocene and Oligocene. As open environments began to replace closed environments during the Middle Miocene, Equidae morphology, like in other ungulate families, began to adapt accordingly. A shift towards a cursorial lifestyle, which is key to survival in open landscapes, is indicated by the evolution of a single toe and increased limb and foot length (Beasley 1903, Orlando 2015). Similarly, a change in diet from browse to graze is (not in exact lock-step) reflected in a gradual increase in the length of the head and neck, and importantly, a major change in dental form (Orlando 2015).

As mentioned above, equid dentition, particularly premolars and molars, have changed considerably in form and function over the course of the last 55 Ma, at times slowly and at other times swiftly (MacFadden 2005a). During the Eocene and through the early Miocene, between 55 and 20 Ma, teeth were short-crowned and adapted for eating leafy browse (Matthew 1926). These earliest horses possessed underdeveloped sheering crests (Fig. 2.1.3) and rounded cusps due to the

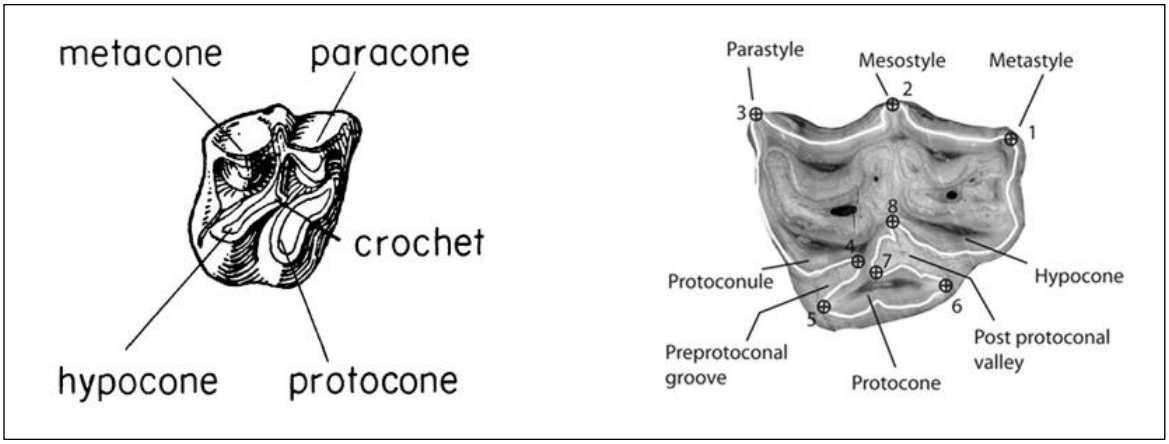



**Figure 2.1.3** Right upper molar (left) of the ancient, browsing pygmy horse *Archaeohippus* showing its simple crest morphology (Woodburne and MacFadden 1982) vs. left upper molar (right) of modern, grazing *Equus* (Seetah *et al.* 2014) showing its larger and more complexly structured teeth.

rarity of grasses (Mihlbachler *et al*. 2011). Following this period, during the later Miocene, between 20 and 15 Ma, the subfamily Equinae appears, ushering in an explosive adaptive divergence in the morphology of dentition, with the shift from the typical brachydont to hypsodont teeth (MacFadden 2005a), better suited for the consumption of fibrous foods like grass.

It has been hypothesised that the evolution of hypsodonty in ungulates came about as a direct response to the aridification of global environments over the course of the Tertiary period (Mihlbachler *et al.* 2011). A gradual thinning of forests and concomitant increase in the presence of grassier plains, required ungulates to adapt over time to the consumption of hard, dry grasses. Hypsodonty, which entails the continuous growth of teeth as occlusal surfaces are worn down through use, was originally regarded as an adaptation only to grazing (Hunt 1995). However, there is now evidence that suggests it is related to the consumption of all plants growing close to the ground, including low-growing shrubs. Hypsodonty thus appears to not only be an adaptation to the corrosive properties of foods such as grass, but also grit that may cover all plants that grow close to the ground (Mihlbachler and Solounias 2006). Still, grass and shrubs tend to grow in open environments, and thus hypsodonty should be regarded as an indicator of open as opposed to closed environments, and not necessarily an indication of the consumption of grass. In addition to an increase in crown height, enamel band folding patterns on the occlusal surfaces of cheek teeth increased in complexity over time, again as an adaptation to the increased abrasiveness of diets (Evans and Janis 2014).

### 2.1.3 The Origins of the Genus *Equus*

Considerable research has focused on determining where and when the lineage that gave rise to all modern horses, zebras and asses began. Orlando *et al.* (2013) sequenced the genomes of different horse breeds, and found that the *Equus* lineage originated 4 – 4.5 Ma. Therefore, all living members within the equid family can be traced back to a common ancestor from this period (Orlando 2015). The existing members of the *Equus* genus are subdivided into four groups – the Caballines or common horses (domestic *E. caballus* and wild *E. przewalskii*), plains zebras (*E. quagga* (now

including previously distinguished *E. burchellii* (George and Ryder 1986, Leonard *et al.* 2005)), *E. zebra* and *E. grevyi*), Hemionines or Asian and Tibetan wild asses (*E. hemionus* and *E. kiang*), and the Asinines or African donkeys (wild ancestor *E. africanus* and domestic *E. asinus*) (Eisenmann 2004, Orlando *et al.* 2009). Today, there are contact areas between *E. zebra* and *E. quagga* in southern Africa (Fig. 2.1.4), and between *E. quagga*, *E. grevyi* and *E. africanus* in eastern Africa (Schulz and Kaiser 2012). However, it is clear that they remain largely separate in habitat. Ancient DNA evidence suggests that the extinct *Equus capensis* may have been part of the plains zebra clade (Orlando *et al.* 2009).

The most recent common ancestor of zebras and asses are known to have crossed the Beringia land bridge about 2 Ma, with their ancestors then expanding over the next 500 000 years and entering Africa twice, independently (Orlando 2015). During the first major glaciation of the late Pliocene, the descendants of this first migration yielded a diversity of zebras that eventually gave rise to the modern zebras that we know today (Hunt 1995). From 2 Ma onwards, there was one or more (since extinct) large-bodied species that became widespread throughout South and East Africa. These large extinct equids included *E. capensis*, *E. oldowayensis* and *E. koobiforensis* (Groves and Ryder 2000).

### 2.1.4 Evaluating Taxonomy in the Fossil Record

Evaluating the taxonomic status of a fossil species is complex, particularly when the taxon in question has a variety of potential morphological/genetic descendants and/or ancestors. Determining what constitutes a species depends on a number of factors specific to the organism,

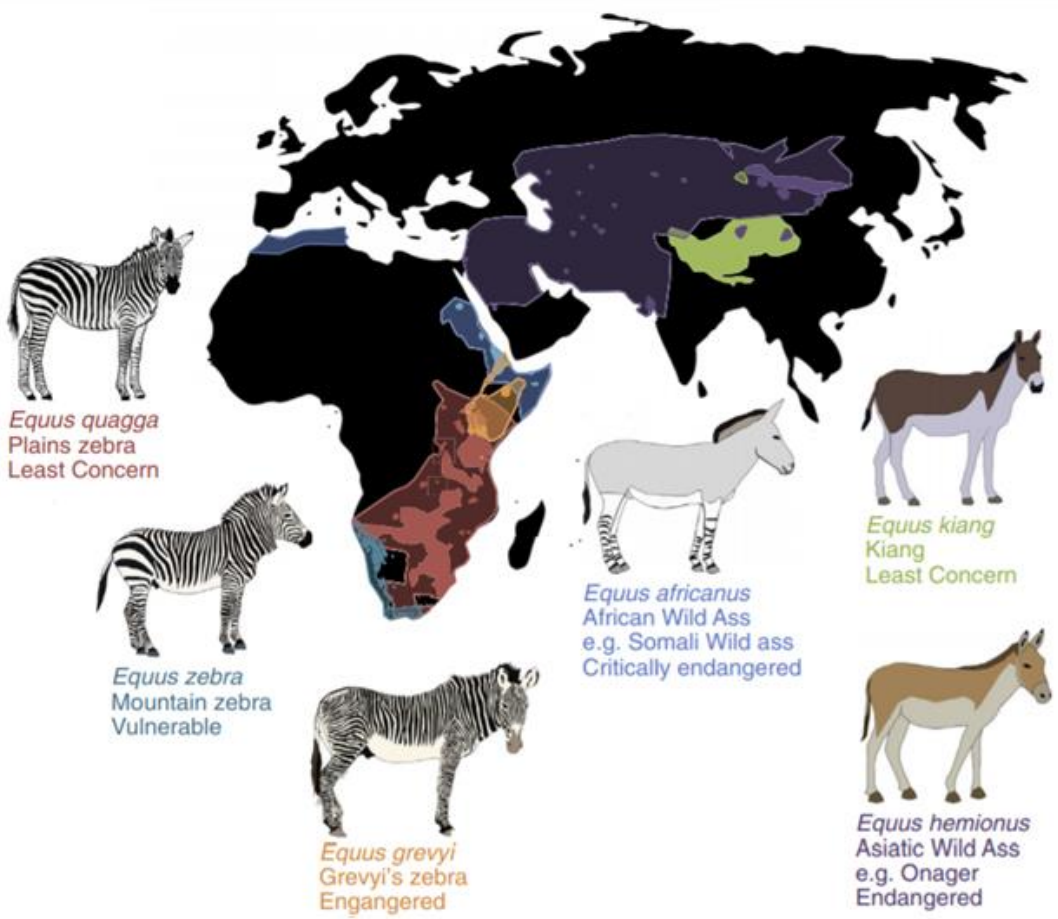



**Figure 2.1.4** Historical (shaded with transparency) and current (shaded with solid colour) distribution ranges of wild extant equids, including each species' status according to the International Union for Conservation of Nature (Orlando 2015).

which in turn means that ideas of species are unlikely to be universally applicable, and what is considered as the most important factors will vary (Miller 2016, Aldhebiani 2018). Due to the complexity of these factors, it may be argued that universal and collective criteria that define boundaries for consistent classification of evolutionary units do not exist (Mishler and Donoghue 1982).

Added to the disputes over a lack of a universal and unambiguous definition for species that can be applied to both the fossil and extant record (Sepkoski 2016), are the personal goals and judgements of the taxonomist. Within so many palaeontological collections, the study of fossils has not always been systematic. *Equus capensis* is an example of this unsystematic investigation and classification of fossils. Studies such as these has oftentimes resulted in a wealth of species delineations that become extremely difficult to tease apart, as well as making later descriptions of additional material near impossible (Cooke 1950, Wells 1959). Throughout the history of taxonomic studies, the cycles of lumping and splitting has been problematic, and ultimately caused the nomenclature of fossil species in the literature to be so confusing and complex (Demere 1986) that revision was clearly necessary. This has been an issue in southern African mammalian studies specifically, and systematic affiliations between species have largely been ignored in favour of naming a new evolutionary entity. Because subjective influence is so prevalent, the identification and estimated number of various taxonomic species will be dependent on the taxonomist's description (Barraclough and Nee 2001, Allmon 2016). It goes without saying that opinions will inevitably vary, causing difficulties with attaining an unambiguous taxonomic status in a fossil group. There is also a lack of correspondence between paleontologists and neontologists (Bennett 1980), as well as paleontologists and each other, and the taxonomy of fossil taxa thereby becomes an exasperating problem, particularly in a field as complex and widely explored as *Equus* taxonomy (Bennet 1980).

The fossil record for extinct taxa is incomplete. Material is often damaged, found out of context, fragmented and/or worn (in the case of dentition). Hence, potential species found within the fossil record, such as *E. capensis*, are notoriously difficult to define (especially in comparison to extant

taxa) (Fig. 2.1.5), and this can arguably be amongst the reasons that taxonomists have historically been able to name new species merely from personal interpretation (Allmon 2016). The naming of *E. capensis* evidences this (Broom 1909, Broom 1928, Cooke 1950). Generally, a species will appear during a single time and at a single place, leaving large gaps in the duration of the presence of many higher taxa (Charlesworth *et al.* 1982). A lack of detailed information of an organism's evolutionary history will consequently cause further issues in terms of classification, and various taxonomically defined species may then only be regarded as an array of hypotheses (Barraclough and Nee 2001, Allmon 2016). While it is evident that pieces

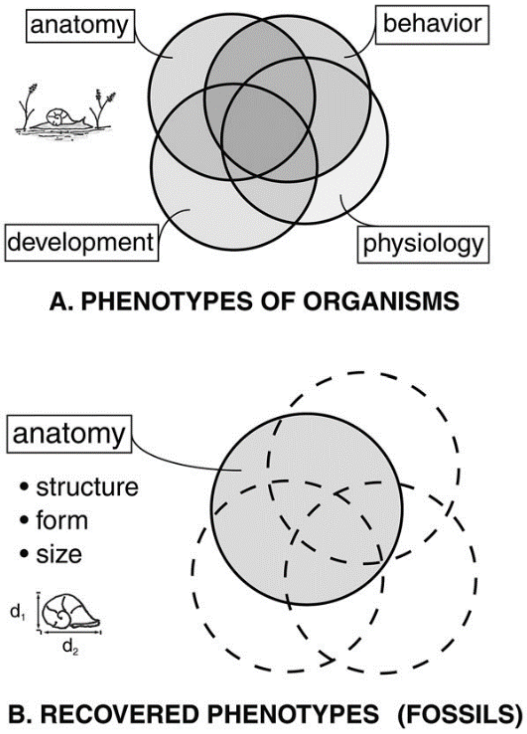



**Figure 2.1.5** Phenotypes of living vs. fossil organisms, evidencing that fossils are mainly comprised of skeletal anatomy, and the other general properties are merely inferred (Miller 2016).

missing from the evolutionary puzzle indeed place limits on the possibility of attaining an adequate solution, it can be argued that a more serious impediment to a holistic understanding lies in the

subjective blocks that then limit conceivable explanations (Gould 1988). A taxonomist may think that a particular feature, for example the curiously large size of *E. capensis* dentition that led to its naming, is worthy of placing a new species on record. In addition, due to the constraint of not having more than a type specimen to go on, this may be seen as sufficient for doing so (Bell 1950).

Extinction plays a large role in the process of taxonomic evaluation if the species being evaluated either is extinct today, or has extinct ancestors. Biological events need to be kept in mind in the analysis of a species' extinction, as these events on their own may have been of equal importance in conjunction with events of physical change (Smith 1989). The absence of changes in environmental conditions does not necessarily mean that there will be no resulting extinction due to physical changes in a species, and it is therefore important to consider both options in determining species extinction. Taxonomic selectivity patterns are the primary methods by which extinction dynamics are described, as they take into account the responses given by certain species to certain geological and environmental events of distress (McKinney 1995). These patterns are valuable for observation as they are able to give indications of what phylogenetically shared characteristics a particular group may have had that enabled them to withstand these events and therefore make them less vulnerable than others.

Extinction is also a vital element to keep in mind when examining speciation, as it needs to be ruled out in the process of extracting information on the speciation and observed patterns of taxonomic groups (Barraclough and Nee 2001). In attempts to taxonomically classify extinct taxa – such as the complicated case of *E. capensis* – living species are one of the chief aspects relied upon to gain information. This is especially the case when the species in question has been named

despite no concrete anatomical or genetic evidence for its classification. It is important to note that speciation events will not be recorded for those that have gone extinct, even though instances of extinction can indeed leave a mark on the overall shape of a species' phylogenetic tree (Barraclough and Nee 2001). At the terminal Pleistocene in Africa, various species of mammals, particularly grazers, went extinct without replacement (Owen-Smith 1987). While *E. capensis* has been claimed to fall amongst these extinct species, questions around its taxonomic status has raised doubts (Peters *et al.* 1992). Widely assumed to be a genetically distinct fossil equid species, recent ancient DNA (aDNA) studies suggest that it may simply have been an extinct morphotype of the extant plains zebra *Equus quagga* (Orlando *et al.* 2009).

In the identification of a taxonomic unit, variation among groups and geographical regions in the rates of speciation are important to consider (Barraclough and Nee 2001). For an extinct entity like *E. capensis*, direct observation is not possible and therefore makes the task a difficult one. Added to this, many extant groups do not have comprehensive enough fossil records that would enable a deeper exploration into these topics. In taxonomic classification, it is crucial to accurately identify when or if the signal indicative of speciation has been lost entirely from present species that have an ancient, extinct ancestor (Barraclough and Nee 2001).

Evaluating the taxonomic status of a fossil species is a complicated task, as is defining a species discovered in the fossil record; and the difficulties that may be encountered come in an array of forms. From biases in the original classification, gaps in the fossil/evolutionary records of taxa, differences in what factors are used to delineate a species, and the effects of speciation and extinction events through time, there is much that must be considered. Clearly one must work

closely and carefully in consideration of all these factors so as to create the most comprehensive understanding of taxa as possible. The large number of species concepts available (Miller 2016) and the nature of the fossil record adds to this difficulty, and one must be clear on the criteria used and the aim of each individual taxonomic study.

### 2.1.5 Issues in Taxonomic Evaluation of Equids

It has often been the case in palaeontology that new species were named on the basis of fairly small skeletal fragments. Morphological differences from previously described species have to be weighed, and it can be difficult to determine how much difference is necessary for defining a new species. Additionally, most early palaeontologists did not have an appreciation of natural morphological variation within equid species (Haughton 1932, Bell 1950, Orlando *et al.* 2009). Typically, all living equids fall into the *Equus* genus (Groves and Ryder 2000); however there have been various instances of populations being placed into discrete genera on the basis of being dissimilar 'enough' to other members of *Equus*. This illustrates the inherent bias in taxonomic evaluation, in which classifications are influenced by the scholars involved, varying identification criteria, as well as the often limited type specimens from the fossil record (Twiss *et al.* 2017). There is a great web of taxonomic and nomenclatural complications within the equid group, and the need for complete systematic revision at the species level is patent.

Despite a general understanding of Equidae family history, the specifics of taxonomic as well as phylogenetic relationships amongst various species of fossil equids are still poorly understood (Orlando *et al.* 2009, Kefena *et al*. 2012). This is largely due to how vast and immense the fossil record really is. During the Pliocene and Pleistocene, there were nearly thirty recognised species

of *Equus*, identified on the basis of either upper or lower tooth morphology (Cooke 1950, Oakenfull *et al.* 2000). With this large number of species, determining their relationship to each other, as well as their relationship to extant *Equus* species becomes problematic. Since then, however, less than half of these have been determined to be valid. Preservation issues further conflate this challenge, as the majority of the surviving evidence is in the form of fragmented bone, on which there are very few species-specific traits (Gilbert *et al.* 1990). While skeletal data may provide plenty of diverse information, particularly in the way of morphology, it does not necessarily provide the resources for the identification of equivalent taxa from the past (Gilbert *et al.* 1990). Eisenmann (2004) has acknowledged that equid "fossil material is rich enough to raise hopes, but not rich enough to fulfill them."

Despite extensive exploration of equid phylogeny through the years, there are still many uncertainties that must be resolved. New evidence constantly pushes researchers to rearrange previously described evolutionary histories and taxonomic categories amongst equids. Perhaps the principal driving force in this is the more recent awareness amongst researchers of the diversity and variation that may exist within a single species of equid. Since the Pleistocene, there has been an evident reduction in taxonomic diversity, and previous cases of taxonomic oversplitting at the species level must thus be considered (Orlando *et al.* 2009). Early palaeontologists have been known to delineate every newly discovered variant as a new species, and a large number of equid species from earlier works have since been reduced to a single species (Haughton 1932, Bell 1950, Cooke 1950, Wells 1959, Gingerich 1974, Churcher and Richardson 1978). It is clear that equid identification has, for the most part, been an interpretative act (Twiss *et al.* 2017), with analysts choosing which specimens to measure and which morphological characters to consider. The

discrediting of so many previous classifications highlights the necessity of reviewing taxonomic classifications as new information is revealed. Previously, discovery of a tooth that did not appear to match another in occlusal or other morphology exactly, would lead to demarcation of an entirely new species. This is a known complication with fossil equids, particularly in southern Africa. Haughton (1932) reviewed what were at the time twenty existing species, and concluded that they may be reduced to just eleven as many of them were named from a single type specimen and/or slight discrepancies between occlusal enamel patterns as a distinguishing feature. Since so many equid species have been erected using qualitative visual analyses of occlusal enamel patterns, Twiss *et al.* (2017) tested the reliability of this method with upper and lower dental specimens of *E. caballus/ferus*, *E. hemionus*, and *E. hydruntinus*. Various specialists visually assessed the equid enamel patterns, and their species assignments were then compared. All zooarchaeologists were given the same criteria (such as protocone and linguaflexid shape), yet every one of them diverged in their species assignations for both mandibular and maxillary teeth. That they were all using the exact same criteria and still produced such inconsistent results, highlights the need for systematic revision within equid taxonomy (Twiss *et al.* 2017). Furthermore, the study draws attention to the variation of enamel pattern within species; some individuals show features that are associated with multiple species, and some show features that are not solidly linked to any species. It therefore falls to the researcher to decide which features to gauge as more meaningful than others.

A well-known example illustrating the scarcity of knowledge around within-species variation in equids is the renewed classification of *Equus burchellii* and *Equus quagga* as a single species, named the latter. A fossil molar from Kromdraai was earlier described as having characteristics of both *E. quagga* and *E. burchellii*, but with the buccal walls slightly convexly rounded and hence

more similar to *E. quagga* than *E. burchellii*, whose walls were described as concave to flattened (Churcher 1970). Clearly, there was an absence of knowledge on the extent of variation allotted within a species' dentition, and DNA evidence has since proved that despite historically assigning numerous fossils from many sites to each species, they are genetically indistinguishable (Faith 2014). MacFadden (2005a: 1728) notes that "the speciation, diversification, adaptation, rate of change, trends, and extinction evidenced by fossil horses exemplify macroevolution" and thus it is vital that we attempt to reconstruct this evolutionary history as accurately and as systematically as possible.

The evolutionary history of *E. capensis* (including its disappearance) is still unexplained and perplexing to a considerable degree. There are conflicting thoughts on the taxonomic status of this giant zebra, with various scholars presenting different theories and species associations (Churcher and Richardson 1978, Eisenmann 2000, Churcher 2006, Orlando *et al.* 2009). Few dental studies have been conducted on it (Churcher 2000), and those that have been performed, have not been systematic. Knowing their value in the phylogenetic reconstruction of equids, systematic investigation into dentition may shed light on where the *E. capensis* belongs taxonomically in this ever-changing and complexly branching tree.

## 2.2 *Equus capensis*

### 2.2.1 Naming of *E. capensis* as a New Fossil Equid Species

In the South African fossil record, the 'Giant Cape Zebra' *Equus capensis* has been characterized as a relatively long-lived taxonomic entity that persisted unaffected from the late Early Pleistocene to the terminal Late Pleistocene (Churcher 2006) and has commonly been classified as an

"unquestionably extinct species" (Klein 1988: 20-21). Prior to its classification as *Equus capensis*, researchers remarked on the bones and teeth of large equids discovered in South African archaeological/palaeontological sites. The assumption was that these were the remains of horses belonging to European settlers, and as a result, they were never critically studied (Broom 1913). The discovery of an ancient mandible belonging to a large equid that was clearly not a domestic horse eventually led to the naming of *Equus capensis* (Broom 1913). Additional remains recovered later allowed for further description of this large zebra as well as the knowledge that it was widely distributed at various Pleistocene sites in southern Africa (Faith 2014).

*Equus capensis* is thought to have been the largest of the African Quaternary equid taxa, standing at 150cm at the withers (the ridge between the shoulder blades) with a body mass greater than 400kg (Faith 2014). Its uniquely large, robust size suggests that it was a bulk grass feeder with a need for a capacious habitat range. Based on fossils from the site of Elandsfontein, the skull of *E. capensis* has a wider muzzle and a shorter distance between its palate and vomer in comparison to *Equus grevyi* (Eisenmann 2000). In terms of limb proportions, *E. capensis* is unlike any equid in the relatively long length of its radius in relation to its third metacarpal (Eisenmann 2000). The proportions of *Equus capensis*' osteology have been recorded as significantly different to that of the modern domestic horse average, with the former more strongly built and roughly a hand (4 inches or 10.16cm) shorter (Broom 1913). Skull remains demonstrate that the head of *E. capensis* is far more robust than the domestic horse as well (Broom 1913). Churcher (1993) states that *E. capensis* descends from *Equus numidicus*. *Equus numidicus* is a species also said to have given rise to the Holocene *Equus grevyi*, a species that Churcher (1993) has stated differs little from *E. capensis* in terms of its morphology.

There have, though, been many incongruities and much confusion historically when it comes to classifying this giant fossil equid. Broom (1909) originally named the species from part of a left lower jaw embedded in a block of limestone found in Yzerplaats, yet did not give a formal diagnosis based on the enamel pattern for naming the species. The mandibular teeth of this type specimen were also not illustrated until Broom (1928) did so, and his reconstructions were based on his personal visualization. All four mandibular teeth contained missing enamel on their occlusal

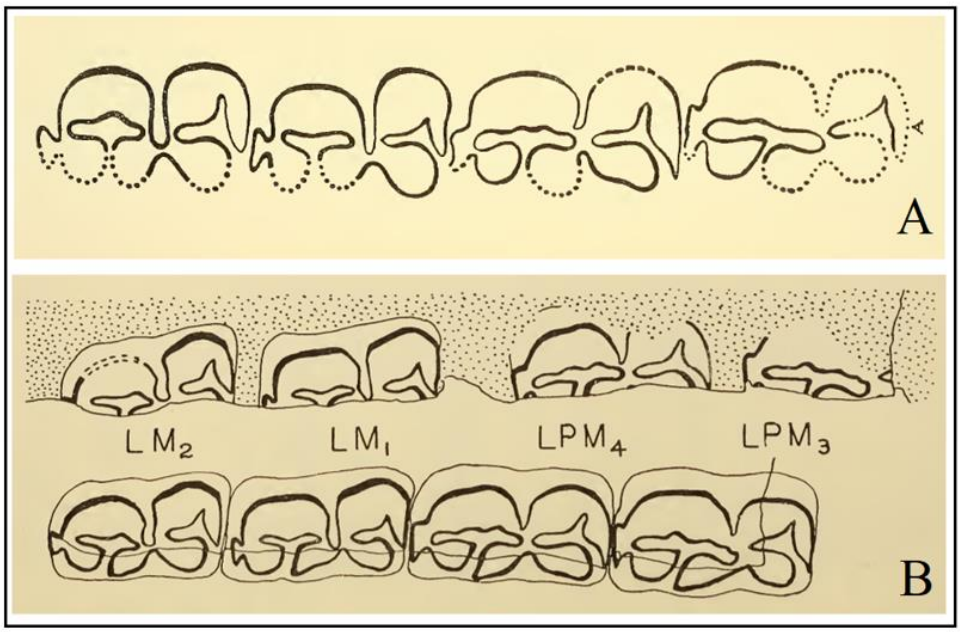



**Figure 2.2.1** A: The first figured images of the type specimen of left lower cheek teeth of *Equus capensis* from Yzerplaats in Maitland (Holocene deposits). The dotted lines represent missing enamel that was presumed (Broom 1928). B: Cooke's (1950) interpretation of the same enamel patterns as they appeared in the limestone slab in 1940 (top image of B is an aerial view of the type specimen as embedded in the limestone).

surfaces, and these patterns were thus extrapolated. Cooke (1950) took issue with Broom's reconstructions and presented his own restoration of what he assumed the missing enamel parts

looked like (Fig. 2.2.1), illustrating marked differences from the original. The species was later described as being its own taxonomic entity due to small plications within the dentition.

The form of the lower teeth have historically been described as most synonymous with the true quagga (Cooke 1950). Since the upper teeth were not decisively known initially, any notably large equid teeth that were found were recorded as *E. capensis*, largely irrespective of their occlusal enamel pattern (Fig. 2.2.2). Once a neotype of the species' upper dentition was described, its form was described as an enlarged version of that of *Equus quagga* (Cooke 1950, Churcher and Richardson 1978). Due to the lack of a formal diagnosis for classifying this species based on dentition, it has also been presumed to be conspecific with a variety of other species of *Equus*, for

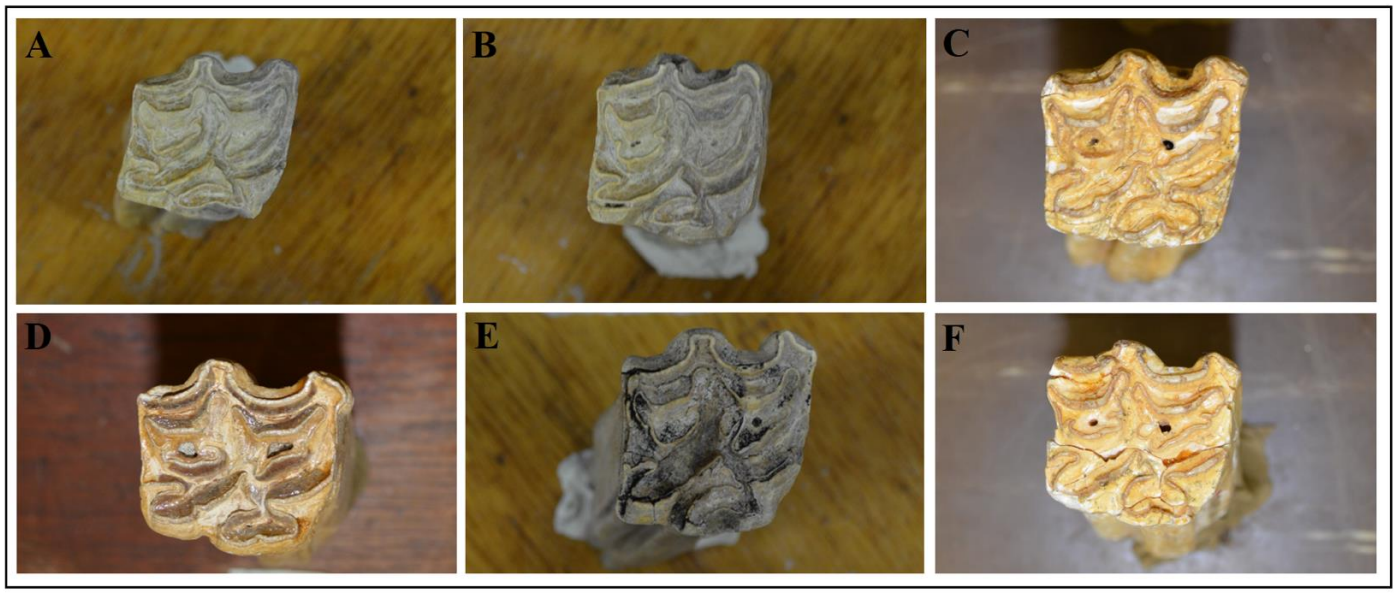



**Figure 2.2.2** Examples of occlusal enamel patterns in maxillary cheek teeth assigned to *Equus capensis* from South African sites. A: Elandsfontein (WCRP2102), B: Elandsfontein (WCRP2100), C: Makapansgat (CoH69), D: Kalkbank (KB1565), E: Elandsfontein (WCRP2110), F: Makapansgat (CoH160).

reasons primarily related to size. Churcher and Richardson (1978) suggested that *E. capensis* is

related to the East African *E. oldowayensis* from Olduvai, basing this on illustrations of enamel patterns that resembled each other. It has also been recorded as a member of the quagga group because, like them, the pli caballine folds were not developed (Haughton 1932). While differing in their osteology, the crowns of the incisors found at Cave of Hearths in Makapansgat, Limpopo were noted as similar to that of *Equus caballus* (as well as *Equus grevyi*) in that they contain heavier buccal than lingual enamel (Churcher 2000). Entire rows of molars were also preserved and examined, with the most reliable feature amongst these lower teeth being the "inflation of the metaconid, metastylid and entoconid enamel outlines, with thick enamel, and usually simple enamel floors to the flexids" (Churcher 2000: 107). This characteristic is said to differentiate *Equus capensis* from *Equus quagga*. However, Churcher and Richardson (1978) state that the form of *E. capensis*' upper dentition is in fact very similar to *E. quagga*, with the ectoloph halves concaving inwards, the protocone being elongate and oval, and the pli-postfossette clearly marked. They noted that the dentition is essentially an enlarged version of *E. quagga*, and that the extreme hypsodonty and overall massiveness that characterises *E. capensis*' dentition is the main feature not present in *E. quagga* (Fig. 2.2.3).

Also important to note is the historical issue of naming multiple species, with no consideration for possible intraspecific variability:

"The neo-biological definition of a species, incorporating as it does the element of reproductive isolation, causes many paleontologists to reject as inapplicable to their own problems much modern biologic work except in the fields of physical and chemical ecology and comparative anatomy. In so doing they operate without the controls imposed by an awareness of the variability of species, the unlikelihood of two species of the same genus

inhabiting the same ecologic niche, the likelihood that a species is comprised of geographically segregated subspecies, and so on" (Bell 1950: 494).

Cooke's (1950) revision of southern African Quaternary Perissodactyla (including *E. capensis*) found that oftentimes recording new species took preference over revising the existing knowledge

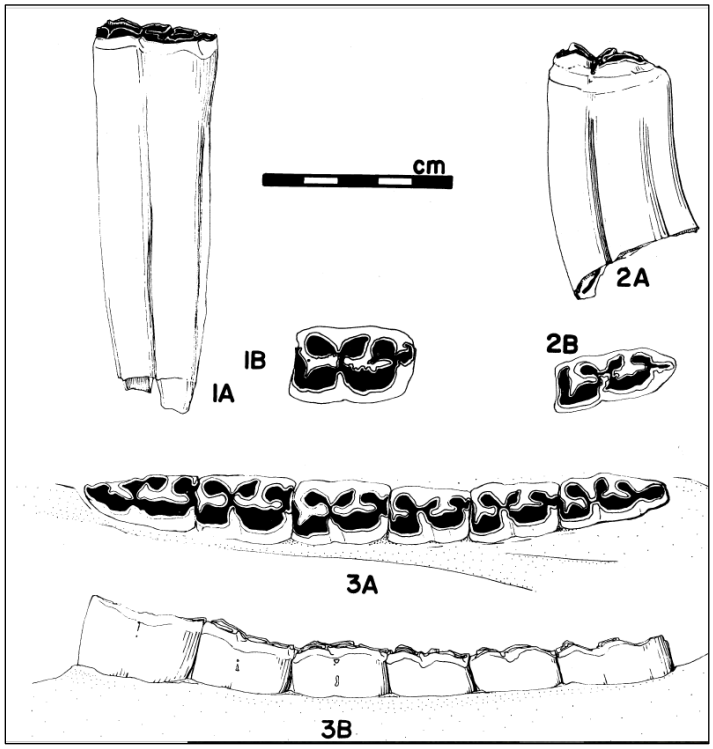



**Figure 2.2.3** 1A & B, 2A & B: Mandibular cheek teeth of *Equus capensis* from the terminal Pleistocene deposits of Elands Bay Cave. 3A & B: Left mandibular dentition of modern *Equus quagga* for comparison (Klein 1974).

of faunal discoveries. Cooke (1950) further highlights the confusion surrounding naming a new species when there is already an extensive array of species names in existence. Therefore, describing a new species is unfeasible unless done so in the context of what has already been named. Wells (1959) elaborated with particular attention paid to nomenclature in southern African equid species' such as *E. capensis*. He pointed out that oftentimes the specimens from which new

species are named are either based on isolated teeth or are defective, which is the case with the *E. capensis* type specimen. It is emphasized that to name a new species on these types of fossils cannot be considered scientifically valid. Wells (1959) further states that various species that have been recorded should in fact be categorized as indeterminable. This includes *Equus capensis*, whose classification is surrounded by ambiguity due to various similar features with other named species.

The more modern classifications for the equid are no simpler, and the taxonomic status of *E. capensis* is disputed today on levels beyond just tooth shape (Faith 2014). Again based on its large size, it has been suggested as conspecific with the similarly large extant *E. grevyi* in East Africa (Eisenmann 2000, Churcher 2006, Faith 2014). Churcher (2014) refers to the two as morphologically identical. However, Eisenmann (2000) compared skull proportions, and deemed *E. capensis* as more similar to *E. quagga* than to *E. grevyi*. The East African *Equus oldowayensis* from the Pleistocene has also been claimed as conspecific with *E. capensis* (Churcher 2014), whereby the former is merely a different name for the East African population of what is the same species. Complicating the matter further, extant *E. grevyi* is thus considered as the surviving form of this East African population, likely conspecific with the ancestral population of *E. capensis*/*E. oldowayensis* (Churcher 2014). While historically *Equus mauritanicus* has been regarded as a subspecies of the extant *E. quagga* (Churcher and Richardson 1978), analysis of various *E. mauritanicus* skulls (Eisenmann and Baylac 2000) found them to be morphologically dissimilar from plains zebras. Interestingly though, *E. mauritanicus* teeth are overtly large and in fact overlap in size with those assigned to *E. capensis* (Faith 2014), leading some to believe that they also may

be related. Overall, it is evident that despite the many advancements in systematics in recent years, the classification criteria for *E. capensis* is still shrouded in confusion and conflict today.

### 2.2.2 Range and Dietary Adaptation

It has been suggested that *E. capensis* was in existence from the late Early Pleistocene to the terminal Late Pleistocene, with a geographical distribution from South Africa, up the African east coast to Egypt (Churcher 2006). Fossils assigned to *E. capensis* have primarily been discovered at sites located across southern Africa, extending across hot, arid regions, coastal zones, as well as areas with both summer and winter rainfall (Badenhorst and Plug 2012). It thus appears that specimens allocated to the species held a broad tolerance in terms of habitat and dietary flexibility. Southern African records show ranges that included the strandveld-dominated coastal areas in the Western Cape, the succulent-dominated interior plains of the interior Karoo, the grassy veld plains in the Northern Cape, the arid grasslands of the southwestern Transvaal (today the North West Province) as well as the grasslands of the western Orange Free State (Churcher 2006). In a broad definition of southern Africa (De Vos 1975) which encompasses Kalaharian, Transvaalian, Zambesian, Basutolian, Cape and Karoo-Namaqualian zones (Fig. 2.2.4), *E. capensis* is known to have been present in all six of these zones (Klein 1980). *Equus capensis* is also noted as having co-occurred with *E. quagga* at the majority of sites where it has been identified in southern Africa (Fig. 2.2.5). This information is intriguing since, in extant equids, co-habitation of more than one species of *Equus* is uncommon (Orlando 2015). While both equids are present at these sites, there is no empirical evidence that states they occupied them contemporaneously. It has been suggested that *E. capensis* entered southern Africa around 1.75 Ma. This is slightly later than it is said to have appeared in East Africa, where apparently its fossil record dates to 1.8 Ma at Olduvai Gorge

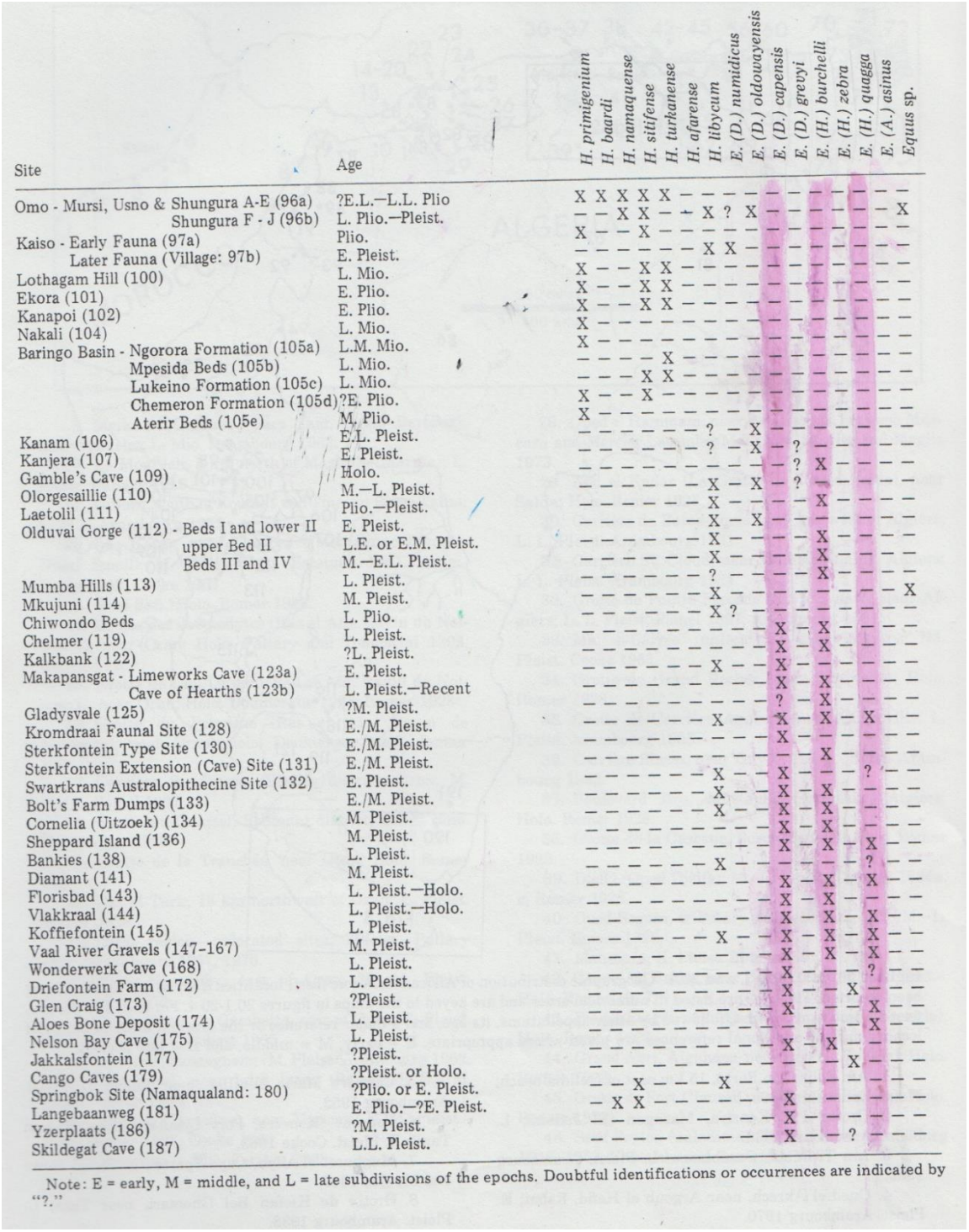
in Tanzania, and 1.9 Ma in the Omo Valley in Ethiopia (Churcher 2000).


**Figure 2.2.4** Ecological zones of Africa (De Vos 1975), all of which have been linked to *E. capensis* at one point or another.

Studies on the dietary adaptation of *E. capensis* specimens have seen conflicting results. Like all modern equids, *E. capensis* has morphological adaptations for grazing, presenting extreme hypsodonty (Faith 2014). Though despite their hypsodont teeth, the taxon has been recorded as mixed feeding as well (Belmaker and O'Brien 2017). Mesowear analysis of 117 *E. capensis* samples (Stynder 2009) showed it to have been a typical grazer, evidently preferring open grassland habitats. Isotopic data support this classification for grazing in the species (Lee-Thorp and Beaumont 1995). Alternatively, also using mesowear analysis (however with only 14 samples), *E. capensis* has been described as a mixed feeder (Kaiser and Franz-Odendaal 2004,

Faith 2012) with a seemingly flexible diet. That this initial mesowear study suggested a mixed feeding diet may in part be due to the unique fynbos vegetation of the area (Kaiser and Franz-Odendaal 2004. Based solely on taxonomic analogy, Klein and Cruz-Uribe (1991) and Klein *et al.* (2007) identified *E. capensis* as an obligate grazer. However, apart from the abovementioned mesowear studies of *E. capensis* (Kaiser and Franz-Odendaal 2004, Stynder 2009), Klein and Cruz-Uribe's (1991) and Klein *et al.*'s (2007) dietary assignations have not been further tested using a method of dietary reconstruction that is independent of taxonomy.

It has been broadly accepted that the species disappeared in southern Africa during the transition from the Late Pleistocene to the Holocene (Plug and Engela 1992, Kaiser and Franz-Odendaal 2004, Thackeray 2010, Faith 2012, Faith 2013, Faith 2014), a period distinguished by a general decline in various large-bodied grazers across southern Africa (Faith 2013). Excavations at Wonderwerk Cave in the Northern Cape province revealed *E. capensis* remains in the earlier Holocene deposits (Thackeray *et al.* 1981, Thackeray 1988), along with various species of known grazing preference. Thereafter, no *E. capensis* remains were recovered in the more recent Holocene layers at the site. That the apparent extinction of the species corresponds with the dramatic terminal Pleistocene environmental changes 12 – 10 thousand years ago (ka) may be of great relevance, as the reduction of open grasslands likely lead to restricted range, as well as restricting the numbers within populations (Klein 1977, Thackeray 1979). The fluctuation of climate and environment during the Pleistocene-Holocene shift evidently played a role in the disappearance of *E. capensis*, with the animal's last appearance coinciding with the large decrease in grassland efficiency after the Last Glacial Maximum (LGM). Further supporting *E. capensis*' last appearance at the onset of the Holocene, is its disappearance at Apollo 11 Cave as well as at Elands Bay Cave, coinciding



| Site | Age | *H. primigenium* | *H. baardi* | *H. namaquense* | *H. sitifense* | *H. turkanense* | *H. afarense* | *H. libycum* | *E. (D.) numidicus* | *E. (D.) oldowayensis* | *E. (D.) capensis* | *E. (D.) grevyi* | *E. (H.) burchelli* | *E. (H.) zebra* | *E. (H.) quagga* | *E. (A.) asinus* | *Equus* sp. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Omo - Mursi, Usno & Shungura A-E (96a) | ?E.L.—L.L. Plio | X | X | X | X | X | – | – | – | – | – | – | – | – | – | – | – |
| Shungura F - J (96b) | L. Plio.—Pleist. | – | – | X | X | – | – | X | ? | X | – | – | – | – | – | – | X |
| Kaiso - Early Fauna (97a) | Plio. | X | – | – | X | – | – | – | – | – | – | – | – | – | – | – | – |
| Later Fauna (Village: 97b) | E. Pleist. | – | – | – | – | – | – | X | X | – | – | – | – | – | – | – | – |
| Lothagam Hill (100) | L. Mio. | X | – | – | X | X | – | – | – | – | – | – | – | – | – | – | – |
| Ekora (101) | E. Plio. | X | – | – | X | X | – | – | – | – | – | – | – | – | – | – | – |
| Kanapoi (102) | E. Plio. | X | – | – | X | X | – | – | – | – | – | – | – | – | – | – | – |
| Nakali (104) | L. Mio. | X | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| Baringo Basin - Ngorora Formation (105a) | L.M. Mio. | X | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| Mpesida Beds (105b) | L. Mio. | – | – | – | – | X | – | – | – | – | – | – | – | – | – | – | – |
| Lukeino Formation (105c) | L. Mio. | – | – | – | X | X | – | – | – | – | – | – | – | – | – | – | – |
| Chemeron Formation (105d) | ?E. Plio. | X | – | – | X | – | – | – | – | – | – | – | – | – | – | – | – |
| Aterir Beds (105e) | M. Plio. | X | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| Kanam (106) | E.L. Pleist. | – | – | – | – | – | – | ? | – | X | – | – | – | – | – | – | – |
| Kanjera (107) | E. Pleist. | – | – | – | – | – | – | ? | – | X | – | ? | – | – | – | – | – |
| Gamble's Cave (109) | Holo. | – | – | – | – | – | – | – | – | – | – | ? | X | – | – | – | – |
| Olorgesaillie (110) | M.—L. Pleist. | – | – | – | – | – | – | X | – | X | – | ? | – | – | – | – | – |
| Laetolil (111) | Plio.—Pleist. | – | – | – | – | – | – | X | – | – | – | – | X | – | – | – | – |
| Olduvai Gorge (112) - Beds I and lower II | E. Pleist. | – | – | – | – | – | – | X | – | X | – | – | – | – | – | – | – |
| upper Bed II | L.E. or E.M. Pleist. | – | – | – | – | – | – | X | – | – | – | – | X | – | – | – | – |
| Beds III and IV | M.—E.L. Pleist. | – | – | – | – | – | – | X | – | – | – | – | X | – | – | – | – |
| Mumba Hills (113) | L. Pleist. | – | – | – | – | – | – | ? | – | – | – | – | X | – | – | – | – |
| Mkujuni (114) | M. Pleist. | – | – | – | – | – | – | X | – | – | – | – | – | – | – | – | X |
| Chiwondo Beds | L. Plio. | – | – | – | – | – | – | X | ? | – | – | – | – | – | – | – | – |
| Chelmer (119) | L. Pleist. | – | – | – | – | – | – | – | – | – | X | – | X | – | – | – | – |
| Kalkbank (122) | ?L. Pleist. | – | – | – | – | – | – | – | – | – | X | – | X | – | – | – | – |
| Makapansgat - Limeworks Cave (123a) | E. Pleist. | – | – | – | – | – | – | X | – | – | X | – | – | – | – | – | – |
| Cave of Hearths (123b) | L. Pleist.—Recent | – | – | – | – | – | – | – | – | – | X | – | X | – | – | – | – |
| Gladysvale (125) | ?M. Pleist. | – | – | – | – | – | – | – | – | – | ? | – | X | – | – | – | – |
| Kromdraai Faunal Site (128) | E./M. Pleist. | – | – | – | – | – | – | X | – | – | X | – | X | – | X | – | – |
| Sterkfontein Type Site (130) | E./M. Pleist. | – | – | – | – | – | – | – | – | – | X | – | – | – | – | – | – |
| Sterkfontein Extension (Cave) Site (131) | E./M. Pleist. | – | – | – | – | – | – | – | – | – | – | – | X | – | – | – | – |
| Swartkrans Australopithecine Site (132) | E. Pleist. | – | – | – | – | – | – | X | – | – | X | – | – | – | ? | – | – |
| Bolt's Farm Dumps (133) | E./M. Pleist. | – | – | – | – | – | – | X | – | – | X | – | X | – | – | – | – |
| Cornelia (Uitzoek) (134) | M. Pleist. | – | – | – | – | – | – | X | – | – | X | – | X | – | – | – | – |
| Sheppard Island (136) | M. Pleist. | – | – | – | – | – | – | – | – | – | X | – | X | – | – | – | – |
| Bankies (138) | L. Pleist. | – | – | – | – | – | – | – | – | – | X | – | X | – | X | – | – |
| Diamant (141) | M. Pleist. | – | – | – | – | – | – | X | – | – | – | – | – | – | ? | – | – |
| Florisbad (143) | L. Pleist.—Holo. | – | – | – | – | – | – | – | – | – | X | – | X | – | X | – | – |
| Vlakkraal (144) | L. Pleist.—Holo. | – | – | – | – | – | – | – | – | – | X | – | X | – | – | – | – |
| Koffiefontein (145) | L. Pleist. | – | – | – | – | – | – | – | – | – | X | – | X | – | X | – | – |
| Vaal River Gravels (147–167) | M. Pleist. | – | – | – | – | – | – | X | – | – | X | – | X | – | X | – | – |
| Wonderwerk Cave (168) | L. Pleist. | – | – | – | – | – | – | – | – | – | X | – | X | – | X | – | – |
| Driefontein Farm (172) | L. Pleist. | – | – | – | – | – | – | – | – | – | X | – | – | – | ? | – | – |
| Glen Craig (173) | ?Pleist. | – | – | – | – | – | – | – | – | – | X | – | – | X | – | – | – |
| Aloes Bone Deposit (174) | L. Pleist. | – | – | – | – | – | – | – | – | – | X | – | – | – | X | – | – |
| Nelson Bay Cave (175) | L. Pleist. | – | – | – | – | – | – | – | – | – | – | – | – | – | X | – | – |
| Jakkalsfontein (177) | ?Pleist. | – | – | – | – | – | – | – | – | – | X | – | X | – | – | – | – |
| Cango Caves (179) | ?Pleist. or Holo. | – | – | – | – | – | – | – | – | – | – | – | – | X | – | – | – |
| Springbok Site (Namaqualand: 180) | ?Plio. or E. Pleist. | – | – | X | – | – | – | X | – | – | – | – | – | – | – | – | – |
| Langebaanweg (181) | E. Plio.—?E. Pleist. | – | X | X | – | – | – | – | – | – | X | – | – | – | – | – | – |
| Yzerplaats (186) | ?M. Pleist. | – | – | – | – | – | – | – | – | – | X | – | – | – | – | – | – |
| Skildegat Cave (187) | L.L. Pleist. | – | – | – | – | – | – | – | – | – | X | – | – | ? | – | – | – |

Note: E = early, M = middle, and L = late subdivisions of the epochs. Doubtful identifications or occurrences are indicated by "?."

**Figure 2.2.5** Selected occurrences of African equid species (Churcher and Richardson 1978). *Equus capensis*, *Equus quagga* and *Equus burchellii* highlighted. If *E. quagga* and *E. burchellii* are recognized as one species as is now understood, and even excluding the possibly erroneous occurrences, *E. capensis* supposedly co-occurs with *E. quagga* at 15 of the 23 sites in which it is present, a considerably large number for a genus whose species do not generally co-exist.

with the aridification of their local environments (Thackeray 1979: 25). The rise in temperature and reduction in rainfall occurred at Elands Bay around 10 000 BP (Before Present), and at Apollo 11 it was around 5000 BP.

As mentioned above, the taxonomic status of *E. capensis* is a controvertible one (Faith 2014), and over the years it has been associated with an array of different *Equus* species based on differing identification criteria. *Equus grevyi* and *E. capensis* have previously been viewed as closely associated; *E. capensis* is documented as the fossil species, and *E. grevyi* as its modern version (Churcher 2006). *Equus capensis* has also previously been loosely distinguished from *E. quagga* based on similarities of dentition as well as both occurring in various sites (Churcher and Richardson 1978). In most sites with *E. capensis* remains, the species is thought to co-occur with its contemporary relatives, *E. zebra* and *E. quagga* (Klein 1980). Interestingly though, *E. capensis* fossils occur more frequently than the smaller relatives in the extremely dry sites. This is probably indicative of its successful adaptation to arid conditions. Almost all large Late Pleistocene equid remains within southern African sites have been assigned to this species (Klein 1980). The varied and oftentimes conflicting conclusions that have been drawn amongst different scholars on the true taxonomic status of *Equus capensis* makes apparent the need for revision, further study and interpretation.

### 2.2.3 Ancient DNA Studies

Ancient deoxyribonucleic acid (aDNA) is DNA molecules that are preserved in ancient biological materials (Brown and Brown 1992). In evolutionary studies, aDNA allows for the study of genetic relationships between extinct organisms and their extant relatives (Bernardo *et al.* 2004). By

enabling this analysis of extinct species, it creates the possibility of directly following genetic changes through time, adding to the knowledge of the evolutionary history of a species (Handt *et al.* 1994; Taylor 1996; Gilbert *et al.* 2005). Variability in sequences of aDNA can provide information on the migrations and diffusions of human and animal populations. Additionally, aDNA from animals at different palaeontological sites can inform on breeding populations (Brown and Brown 1992), and provide insight into the wild origins of domesticated animals such as horses.

Taxonomies of even well-represented extant species are currently being revised due to the introduction of DNA data, thus it is necessary to recognize the possibilities that DNA may offer for ancient animals that have only been studied or classified insofar as their morphology. Existing species are discernably easier to study due to presence of soft tissue, DNA that is modern and thus less likely to be contaminated or damaged, and larger assemblages to compare. Yet still, determining the accurate taxonomic status of extant species is complex, and DNA has led to various taxonomic revisions. Thus, correctly defining taxonomies are even more complicated with fossils. The introduction of aDNA analyses, however, has provided the possibility to place imperfectly represented fossil species such as *E. capensis* within an accurate taxonomic category.

If DNA evidence for a given species correlates with systematic morphological evidence, taxonomists could say with relative certainty where said species exists on a phylogenetic tree. This, however, is rarely the case. For example, morphological analyses suggested a polyphyletic origin of the genus *Equus,* yet mtDNA studies indicated that this was certainly not the case (Fig. 2.2.6) (Forsten 1991a). Rather, it appears the modern morphology of extant *Equus* evolved in the Pleistocene, and was brought about as a response to the period's sharp climatic changes (Forsten

1991a). The incompleteness of the fossil record, coupled with the difficulty in defining equid species amongst fossils (Forsten 1991a), make these inconsistencies not entirely surprising. Added to this, based on dental criteria, in prehistoric southwest Asia it was believed that three species of wild equids existed; *Equus ferus*, *Equus hemionus* and *Equus hydruntines* (Twiss *et al.* 2007). Using aDNA mitochondrial sequences, Orlando *et al.* (2009) determined that the latter two species may not be genetically separate at all. This is further indicative of the space for morphological variability in equid species without there being a change in the overall genetic makeup.

Since its inception, aDNA has provided researchers with a new methodology with which to test species relationships and taxonomies irrespective of evidence from the fossil record. Furthermore, with the progress made in aDNA studies over the years, it is possible for it to be extracted from an array of materials (Brown and Brown 1992). The first extraction of aDNA molecules was in fact paleontological in its nature, with Higuchi *et al.* (1984) extracting and cloning aDNA from dried muscle of *Equus quagga* and analyzing 229 base pairs of the mtDNA (Brown and Brown 1992, Soltis and Soltis 1993, Thackeray 2010). The presence of aDNA in dried tissues is well-established, and may now be extracted from humans, animals, bog and plants. It is of course easier to conduct these studies when there are several specimens of a particular species, when the analyses are able to be reproduced to confirm results, and when controls and criteria are followed so as to avoid contamination (Handt *et al.* 1994).

Contamination is and has always been a chief limitation in aDNA extraction and analysis. DNA extracted from ancient archaeological remains is often contaminated with modern, microbial DNA due to the bones becoming infested with bacteria, fungi and algae whilst they are in the ground,

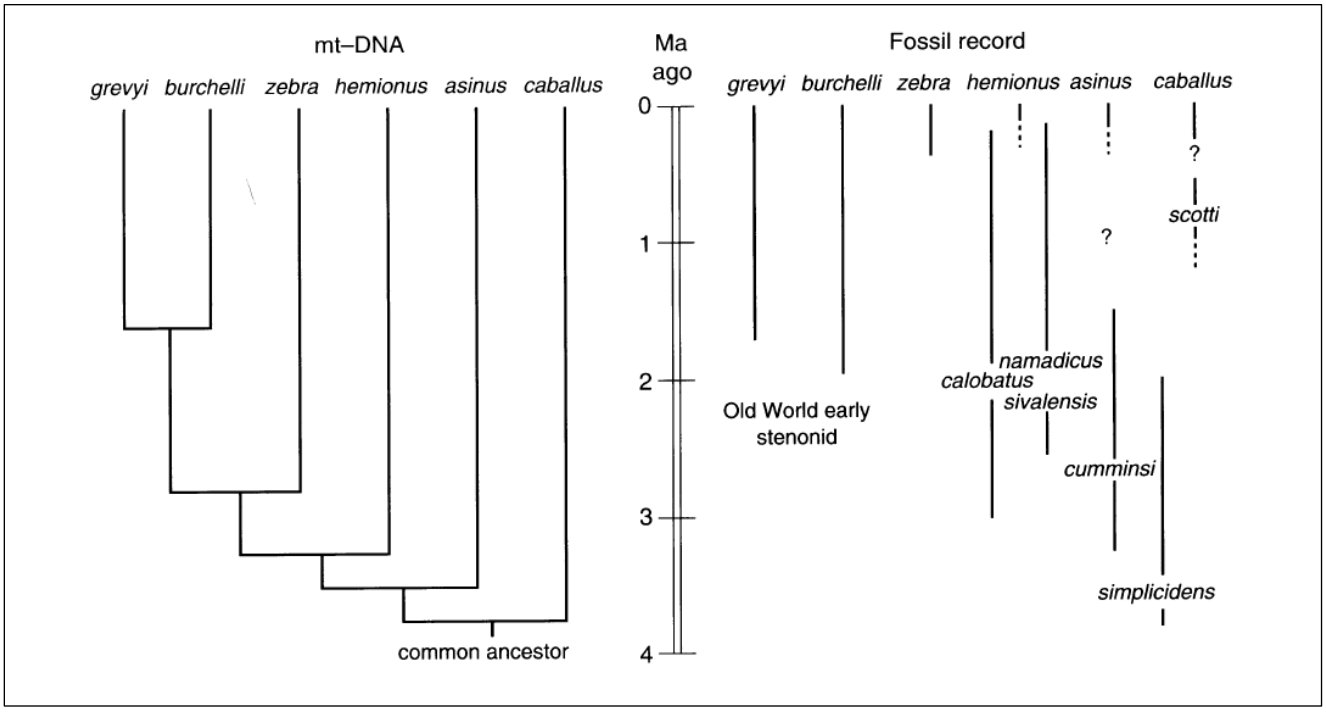



**Figure 2.2.6** Tree of extant species of *Equus* based on mtDNA cleavage maps (George and Ryder 1986), and the fossil record; whereby the continuous lines represent the known fossil record and spotted lines are referred fossils. Branching-off dates between species are at points in close agreement (e.g. *E. grevyi* and *E. burchellii*) and at others mtDNA shows higher branching-off dates in comparison to the fossil record (Forsten 1991a).

and the problem may also then be amplified by additional infestation taking place post-excavation (Brown and Brown 1992). While the addition of microbial DNA into the aDNA does not affect the nucleotide sequence of the aDNA, it does make attempts to determine how much aDNA is present and how much has degraded far more complex (Brown and Brown 1992). Added to this, while it is valuable to quantitate the number of endogenous molecules in an aDNA extract to determine the state of preservation, the presence of fungal and bacterial DNA often overrides the endogenous DNA. This makes straightforward quantitation somewhat fruitless (Handt *et al.* 1994), especially when it comes to extinct species that are not widely available for analysis. The quality

of preservation in *E. capensis* aDNA has been observed as fairly poor, with Orlando *et al.* (2009) able to extract uncontaminated aDNA from just four teeth in their study of equid evolutionary history.

aDNA studies evidently have their limitations. For one, it is difficult to use aDNA to assign biological and physical characteristics to fossil samples, as complex traits such as height or body size have historically been paid less attention than genes involved in biochemical processes such as metabolism (Brown and Brown 1992). Hence, aDNA studies will not specify if a bone is from a small or large individual, and morphological differences will not equate to discrete species delineations as they so often do in the fossil record, unless they are truly genetically distinct. Such complex morphological traits are also plastic, and reliant on the specimen's diet and environment.

aDNA analyses have been applied in various equid studies, oftentimes presenting interesting and unexpected results when compared to the fossil record. Vilà *et al.* (2001) conducted a sequence analysis of equids that included modern, historical and Pleistocene samples. The results of the research indicated a diversity of matrilines that were not due to an ancient domestication event or an accelerated mutation rate. Construction of a phylogenetic tree showed that ancient specimens were more similar than previously assumed to modern horses (Vilà *et al.* 2001, Bernardo *et al.* 2004). This study indicated that domestic horses are of an ancient lineage, and that the 6000-year-old origin of domestic horses presented via the archaeological record means that many matrilines must have been incorporated into the gene pool of what is today the domestic horse breed (Vilà *et al.* 2001).

Orlando *et al.* (2009) conducted a DNA analysis on a range of extinct equids, revealing evolutionary patterns that differed from results of previous studies. *Equus capensis* was one species included in the analysis (*N*=4), with the aim of addressing its phylogenetic relationship to other zebra species and to help locate its contested taxonomic position. The implications of their results call for revisions at the generic, sub-generic as well as species levels of Equidae taxonomy. The sequences from *E. capensis* dental samples formed a clade within the modern plains zebra species (including extinct *Equus quagga*). *Equus capensis* clustered amongst the two southern subspecies *Equus burchellii* and *Equus quagga* (Orlando *et al.* 2009), which are now confirmed as genetically identical and named *Equus quagga*. Thus, the study proposes that *E. capensis* be placed in the same taxonomic group as the plains zebra *E. quagga*. The genetic distance that was exhibited between extinct *E. capensis* and extant plains zebras were within the range of the intraspecific diversity that has been found within most other zebra species (Orlando *et al.* 2009). It is also important to note that the plains zebra group was found to be incredibly plastic (Orlando *et al.* 2009, Thackeray 2010), since they are able to adapt morphologically if called for by selective pressures, whilst still retaining the same overall DNA structure. This would have inevitably been the case during the climatically and environmentally tumultuous Pleistocene in Africa. The marked plasticity of this zebra group likely caused taxonomists to place morphologically dissimilar variants into separate species categories, when in fact the DNA shows that this is likely not accurate. The findings that this DNA study produced greatly contrast Churcher's (1986) claims of *E. capensis* being conspecific with its extant descendant, *E. grevyi* (Thackeray 2010). *Equus grevyi* appeared to be genetically more closely connected to Asian asses and in no way related to *E. capensis*, despite morphological similarity in size. The proportions of *E. capensis*' skull also show a close affinity with the true Cape quaggas, an observation that is in agreement with the genetic

findings (Orlando *et al.* 2009*)*. Using the skull as a taxonomic indicator, this is further suggestive that *E. capensis* formed part of the same taxonomic group as phenotypically plastic plains zebras (Orlando *et al.* 2009).

There is no doubt that aDNA studies provide researchers with new and interesting discoveries on the inter-/intra-relationships of species, oftentimes calling for reconsiderations of what the literature has previously asserted. In evolutionary studies, while valuable, it is evident that when used to determine species taxonomy as well as the relationships within and between related species, aDNA has various drawbacks that need to be considered, particularly in terms of the age of specimens. The older a specimen is, and the lower the quantity of samples available (age typically informs quantity of accessible material), the less feasible aDNA studies are as methodological options for taxonomic analyses. *Equus capensis* is hypothesized to have originated almost 2 Ma (Churcher 2006), so given the current methodological limitations associated with aDNA only the more recent specimens have the potential to be analysed. Despite its shortcomings, aDNA has provided palaeontologists with a fresh way of looking at fossil species and their relation to each other, and has oftentimes led to revisions of phylogenetic relationships that were previously seen as incontrovertible based on fossil occurrences. aDNA has placed doubt on prior classifications of species such as *E. capensis*, which then necessitates the use of additional methods, such as dental morphology for a more comprehensive study.

## 2.3 Global Climate Change Over the Last Five Million Years

### 2.3.1 Mid-to Late Pleistocene Climatic fluctuations

The past 5 million years have been characterized by a distinct shift in climate, as the onset of the Pliocene marked a transition to colder conditions, with increasingly marked cycles of glacials and interglacials (Potts 1998a). In contrast to the warmer, more stable climate of the Miocene epoch, more droughts began to occur the Pliocene, and the increase in seasonality and climatic instability continued to heighten in the Pleistocene (Tankard and Rogers 1978, Van Zinderen Bakker and Mercer 1986, Potts 1998a). Globally, the mid-to late Pleistocene was one of the most climatically unstable periods in time (Fig. 2.3.1), where fluctuations between glacial and interglacial periods

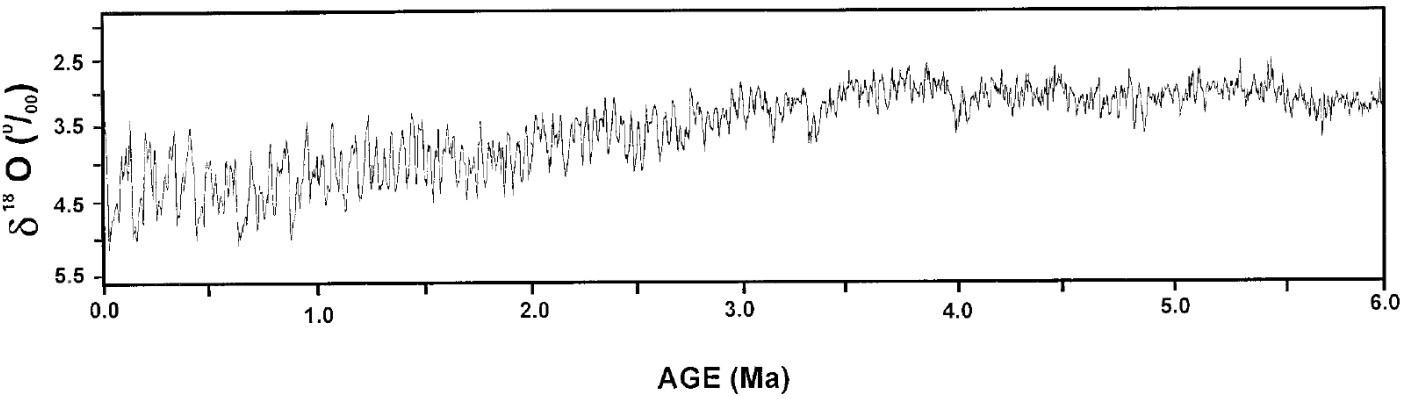



**Figure 2.3.1** Isotopic record from deep sea cores for the last 6 million years (Potts 1998a). The $\delta^{18}O$ measurement is a proxy of global glacial ice volume and the temperature change related to it. An overall trend of cooling is shown, particularly since around 3 Ma. Important to note is the increase in climatic fluctuations over time, particularly from 1 Ma onwards.

were exaggerated and rapid (Barnosky 2005, Lehmann *et al.* 2016). These fluctuations profoundly affected plant and subsequently animal communities around the globe (Potts 1998b, Barnosky 2005) and provided the background for the emergence of *E. capensis*. Around 3 Ma, at the onset of the Pleistocene, glacial conditions in Africa encouraged the expansion of open grasslands at the expense of closed bushlands. Interglacials had the opposite effect, but environments did not revert back to bushlands during interglacials. While bushes and shrubs would have begun to recover

during interglacials, overall declining global temperature made sure that environments did not return to Miocene type woodlands (Scott 2002). Interglacials were generally characterized by comparatively wetter and warmer conditions and an increase in $C_3$ vegetation (such as shrubs and bushes), whereas glacial periods were marked by cooler, more arid conditions and increased contributions of $C_4$ vegetation, particularly arid-adapted grasses (Castañeda *et al*. 2016). During the last 500 000 years especially, records have shown even stronger disparities between warm and cold periods of the Pleistocene.

### 2.3.2 Effect of the Climatic Shifts on Animal Communities

The length of glacial and interglacial periods were significant, as species turnover and/or adaptation was less likely to happen when glacial periods were too short to allow for species to respond accordingly. The onset of the Middle Pleistocene, around 781 ka, ushered in glacial cycles of 100 000 years (Schefuß *et al*. 2003, Herries 2011). During these times, the global ice volume greatly increased, leading to considerable distress of the climate system (Schefuß *et al.* 2003). Preceding this transition, glacial cycles were less than half the length, lasting about 41 000 years. Unsurprisingly, the mid-Pleistocene climatic shifts, particularly the extended glacial periods, had a profound effect on the biology of mammalian communities.

Natural selection is the process whereby species adapt and evolve physically as well as genetically in response to changes in their environment (deMenocal 2004). Pleistocene fossil records clearly show the effects of natural selection with mammalian species from across the globe having responded physically to fluctuations in climate (Guthrie 2003, Searle *et al.* 2009). The emergence of comprehensive paleoclimatic records in recent years has provided the climatic background

against which scientists are able to evaluate the evolutionary changes apparent in the fossil record (deMenocal 2004).

With more defined differences between glacial and interglacial periods, adaptability and flexibility became key in animal lineages during the Pleistocene. These climatic changes presented themselves in a variety of ways. Some were apparent, such as mean annual temperature or rainfall; and others were subtler, such as seasonality changes, monsoonal activity and shifts in vegetational assemblages (Barnosky 2005). It is the accumulation of these recurrent shifts that lead to adaptive specializations in Pleistocene fauna (Fig. 2.3.2).

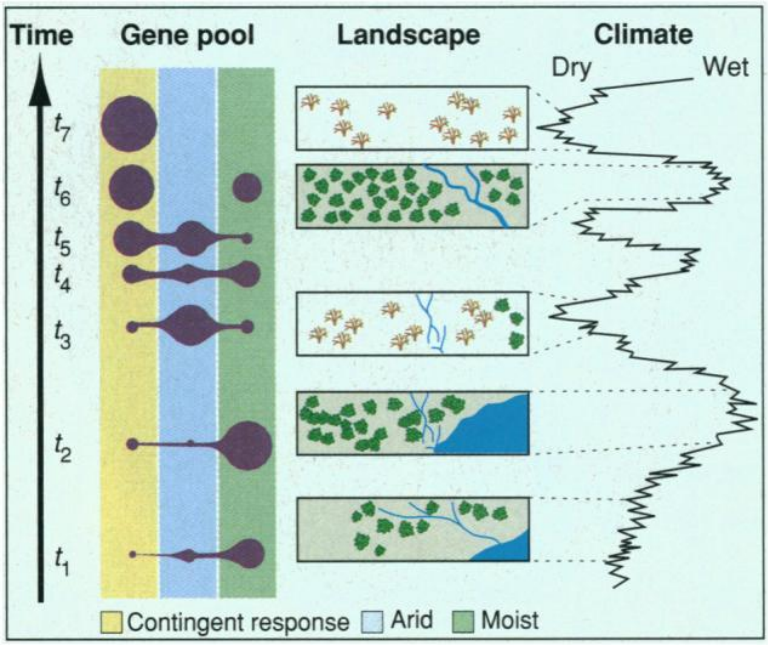



**Figure 2.3.2** Variability selection in a group of organisms that share a common gene pool (Potts 1996). Variation in climate is reflected by fluctuations in vegetation (Landscape). At $t_1$, a river feeds a lake in an open woodland. Surface water disappears after climatic extremes ($t_7$), and different phenotypes within the organism's gene pool are divided. These are separated into features that favour moist and highly vegetated environments (green), those that favour dry and open habitats (blue), and contingent responses which are depended on environmental input (yellow).

Mammalian groups living in Africa during the Middle and Late Pleistocene responded to the climatic fluctuations in various identifiable ways. Within the global context of Late Pleistocene mammalian extinctions, Africa was by far the least affected continent (Fig. 2.3.3). Interestingly, the most dramatic changes in faunal distribution in southern Africa occurred along the southern and southwestern coasts of South Africa (Klein 1986), where the majority of the *E. capensis* samples come from. During the warmer interglacials, browsing and mixed feeding ungulates were

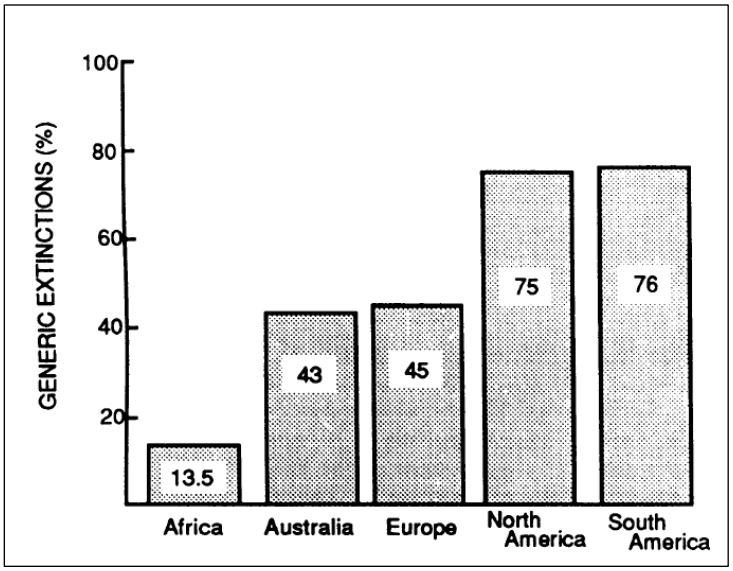



**Figure 2.3.3** Geographic distribution of Late Pleistocene extinctions of mammalian large herbivore genera (including all extinctions during the last 130 000 years of the Pleistocene of genera with body masses (> 5 kg) (Owen-Smith 1987).

relatively common here, but became scarcer during the colder periods. Overall though, grazers were always common which is a reflection on the overall cooler temperatures of the Pleistocene (Klein 1986). It has also been observed that the grazing faunas of the Pleistocene were inclined to be large-bodied (Klein 1975, Klein 1986, Peters *et al.* 1992, Faith 2014).

Phenotypic plasticity, producing adaptability in body size within a species, has previously been paid less attention than genotypic differences in body size (Hutson and Wolverton 2011). However, phenotypic plasticity is at the core of an animal's ability to react to climatic inconsistencies (Pfennig and Pfennig 2009). The ability of an animal to shift its phenotype in response to climatic alterations is what can shield populations from becoming extinct, and is thus imperative to investigate in species that survived climatically tumultuous stages in the fossil record. Developing phenotypic plasticity as a mechanism for survival during periods of great climatic turbulence could be the chief explanation for the morphological diversity that exists in certain taxonomic groups (Pfennig and Pfennig 2009, Ozgul *et al*. 2009).

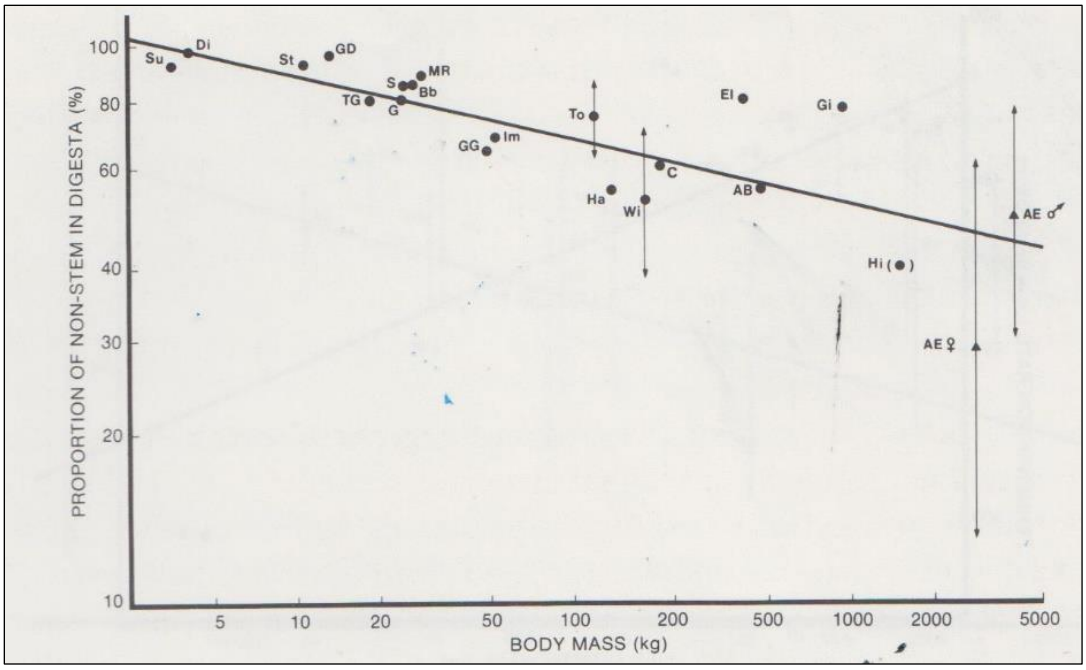



**Figure 2.3.4** Proportion of non-stem material (leaves, fruit, etc.) in the stomach contents of various large herbivores in relation to body mass (Owen-Smith 1988). Circles: Foregut fermenters. Triangles: Hindgut fermenters.

2.3.3 Responses of the Equid Family to Pleistocene Climatic and Environmental Shifts

As temperatures began to fall during the Pleistocene, $C_4$ grasses began to dominate landscapes, reaching peaks in abundance during glacial periods. Interestingly at approximately this time, many large-bodied ungulates, including several equid species, also appear in mammalian fossils records (Owen-Smith 1988). It has been suggested that large body size in part developed in certain ungulate species as a response to the lower digestibility of $C_4$ grasses (MacFadden 2005b) (Fig. 2.3.4). Large bodied ungulates have longer gut retention times, which increases digestive efficiency of low digestible foods (Owen-Smith 1988, MacFadden 2005b).

With the onset of the Holocene and warmer temperatures, grasslands began to recede as shrubs/trees started to dominate plant communities. The decrease in available grass resources seriously affected ungulate diversity as large-bodied bulk grazers began to struggle and eventually die off. Large-bodied equids that disappeared from the African fossil record around this time included *E. oldowayensis*, *E. mauritanicus* and *E. capensis* (Potts 1988a, Faith 2014). Significantly, smaller-bodied ungulates, including equids such as the plains zebra (*E. quagga*), persisted. Dietary proxies such as dental microwear analysis indicate that these survivors invariably consumed a generalist diet composed of both graze and browse. Small body size and dietary flexibility thus appear to have been key to survival in the increasingly mosaic environments of the Holocene (Rivals *et al*. 2009, Semprebon *et al.* 2016).

## 2.4 Depositional Contexts of South African *Equus* Fossils

Equid fossils have been discovered at a variety of archaeological sites across South Africa, the majority of which are included in this research (Fig. 2.4.1). Almost all of these sites have presented

chronological challenges that make it difficult to securely date their faunal assemblages (see appendix A for a breakdown of each site). This situation complicates attempts to evaluate the taxonomic validity of South African fossil mammal species like *E. capensis*.

Many South African fossil/archaeological sites are open-air and as such are notoriously difficult to date (Kuman 1998). Open-air sites also present complications in demonstrating direct association between various finds (Carrión *et al.* 2000), and one often needs to take an educated guess as to whether fossils are contemporaneous or not. In these instances, oftentimes the sites will be recorded but not properly dated, and their contexts are not properly understood. Additionally, it is often simply assumed that materials that are closely associated are concurrent (Klein 1988), when in fact their close physical proximity could be the result of an array of taphonomic factors. Mixture of material is also a confounding issue, where it is often not possible to determine if materials belong to separate sequences (Klein 1988), if they occurred along one continuum, or if they occurred together in one sequence that has been disturbed. Postmortem transportation of fossil material is a chief source of bias, where what may be multiple communities can intermingle and appear as one (Peterson 1977). The sporadic accumulation of material greatly complicates analyses, as fossils found in close association may be interpreted as contemporaneous, when in fact they may be from completely different time periods (Hendey 1974). As well as the ages of various fossils found in open-air sites being unknown, much of the stratigraphy in southern African sites is disturbed and layers are not clearly defined as they can be in East Africa – this often leads to the possible ages of fossils being extremely broad, and stratigraphic relationships between materials nearly impossible to verify (Carrión *et al.* 2000).

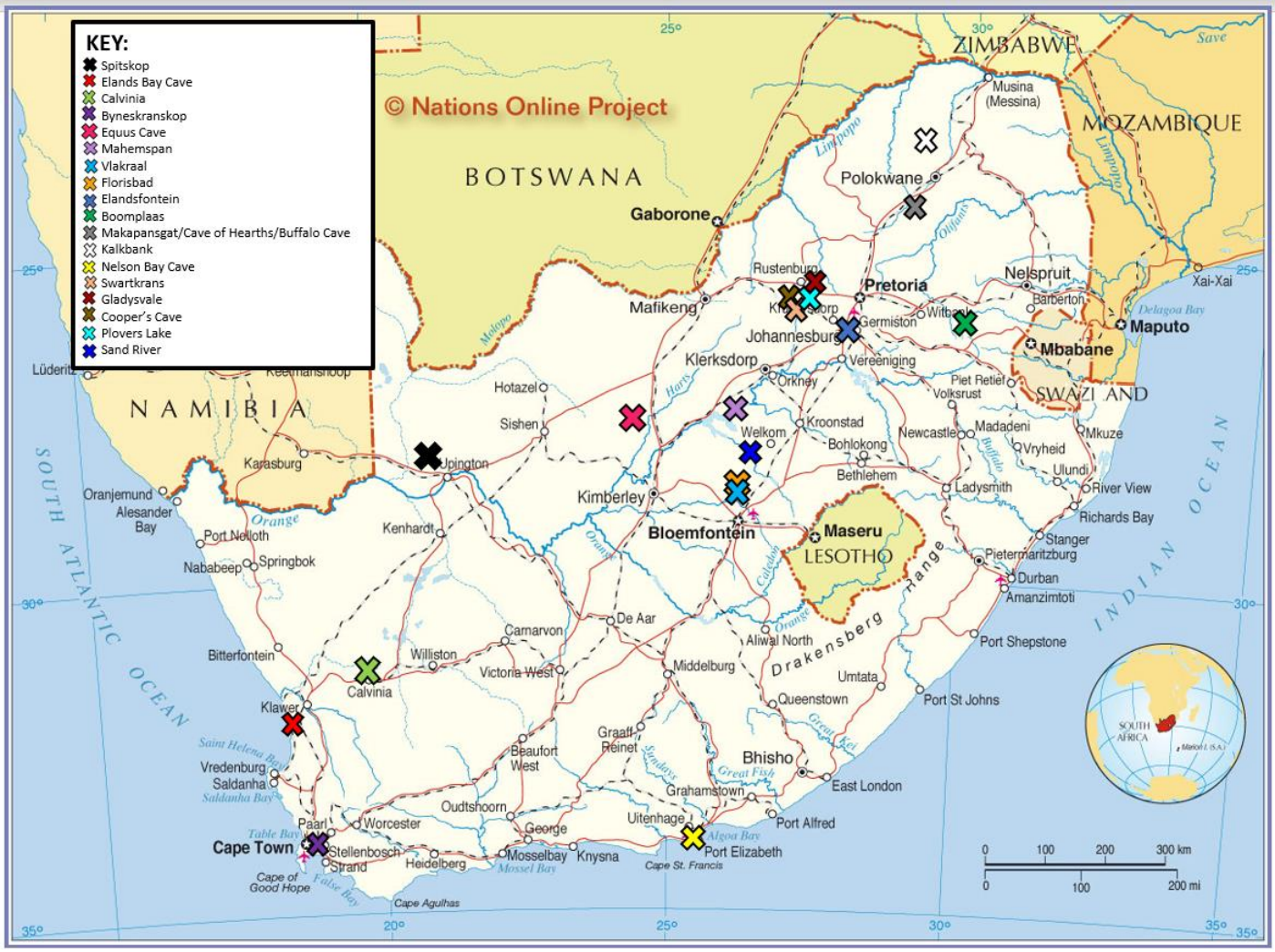



**Figure 2.4.1** Map of South Africa showing sample site locations of this research (https://localdemocracy.net/countries/africa-southern/south-africa/).

The concerns surrounding dating open-air sites and their fossils are evident, however cave sites on the subcontinent also present their own issues. They are known to have limited lifetimes, may be flushed of previous deposits, and, specific to southern Africa, the bedrock lithologies present do not favour preservation (Klein 1988). Added to this, many cave sites are made up of multiple small caves that should essentially be studied as separate sites. It is imperative that these distinctions are made in the literature when referring to where a fossil comes from as there are bound to be separate

**Table 2.1** Summary of site ages and the methods used to determine them (including four East African sites included in this research).

| Site | Time Period | Dating method | Geographic Region |
|---|---|---|---|
| **Elands Bay Cave** | >40 000 - 300 BP (Cartwright and Parkington 1997) | $^{14}C$ | West Coast, SA |
| **Elandsfontein** | 1Ma - 600ka (Klein *et al.* 2007) | Taxonomic composition of large mammals | South-Western Cape, SA |
| **Boomplaas** | 51 200 (±2600)BP - 11 930 (±50)BP (Pargeter *et al.* 2018) | $^{14}C$ | Western Cape, SA |
| **Nelson Bay Cave** | 23 355 - 5730 BP (Loftus *et al.* 2016) | $^{14}C$ | Western Cape, SA |
| **Byneskranskop** | 17 105 - 1870 BP (Loftus *et al.* 2016) | $^{14}C$ | Western Cape, SA |
| **Vlakkraal** | Middle Pleistocene (Ecker and Lee-Thorp 2018) | Unknown | Western Cape, SA |
| **Florisbad** | 300 - 100 ka (Ecker and Lee-Thorp 2018) | ESR & OSL | Free State, SA |
| **Spitskop** | Late Pleistocene (Ecker and Lee-Thorp 2018) | ESR | Limpopo, SA |
| **Equus Cave** | 28 000 - 10 000 BP (Johnson *et al.* 1997, Ecker and Lee-Thorp 2018) | $^{14}C$ | North West, SA |
| **Calvinia** | Unknown | N/A | Northern Cape, SA |
| **Mahemspan** | 12ka & 13-17ka (Brink 2005, Ecker and Lee-Thorp 2018) | ESR | Free State, SA |
| **Cave of Hearths** | 780 ka - Unknown (Wurtz 2011) | Archaeomagnetism | Northern Cape, SA |
| **Buffalo Cave** | 1.07 Ma - 780 000 (Herries *et al.* 2006) | Paleomagnetism & mineral magnetism | Limpopo, SA |
| **Coopers D Cave** | 1.5 Ma - 1.4 Ma (de Ruiter *et al.* 2009) & 1.6 MA - 1.9 Ma (Berger *et al.* 2003) | U-Pb & Faunal association | Gauteng, SA |
| **Kalkbank** | Late Pleistocene (Hutson 2006) | Associated stone tools and fauna | Limpopo, SA |
| **Makapansgat** | 2.9 Ma to 3.32 Ma (McFadden *et al.* 1979) | Paleomagnetism | Limpopo, SA |
| **Swartkrans** | 11 ka - 1.6 Ma (de Ruiter 2003) | $^{14}C$ & ESR | Gauteng, SA |
| **Plovers Lake** | 92.1 (±7.5)ka & 62.9 (±1.3)ka - 88.7 (±1.6)ka (de Ruiter *et al.* 2008) | U-series & ESR | Gauteng, SA |
| **Gladysvale** | 578 ka - 830 ka (Lacruz *et al.* 2003) & 570 ka - 7 ka (Pickering *et al.* 2007), | ESR & U-series | Gauteng, SA |
| **Olorgesailie** | 1 Ma - 500 ka (Deino and Potts 1990) | Single-Crystal 40Ar/39A | Eastern Rift Valley, Kenya |
| **Amboseli** | 2650±85 cal BP - 140±101 (Rucina *et al.* 2010) | $^{14}C$ | Rift Valley, Kenya |
| **Kisaaka** | 94ka - 33ka (Blegen *et al.* 2015) | $^{14}C$, OSL & Uranium-thorium | Central Province, Kenya |
| **Onge** | Unknown | N/A | Central Province, Kenya |

localities, caves, and of course layers or members. Thus, discussing and comparing excavated remains from site to site does not account for the large range of possible temporal distinctions that may exist between and within sites (Herries and Adams 2013).

Overall, there has been a "chronological haze" (Jacobs *et al.* 2008: 733) in dating many southern African sites. This has been the result of different sample preparation methods, different measurements and data analyses, and different sites being dated by different methods (Table 2.1). Added to this, oftentimes one method presents dates that do not correlate across dating laboratories, depending on different calibration standards (Jacobs *et al.* 2008). Noteworthy is that many of the sites in the subcontinent have relied upon U-series and radiocarbon methods to determine their ages, and more recent studies have in fact shown these to be often unreliable dating methods, susceptible to recrystallization as well as leaching (Chase and Meadows 2007). There are also known complexities involved in ESR dating, such as the averaging of ages from material that likely comes from different deposits through mixing, producing multiple age ranges, or not taking context into account which in turn effects the dosimetry (Herries and Adams 2013). Furthermore, material from much of these sites was recovered many decades ago when the modern dating methods that exist today were not available, so relevant samples from a given deposit are no longer accessible for dating (Rightmire 1975). Effectively, what is needed at every southern African site is an approach of multiple dating methods, in which the entire history within a given locality can be recovered, cross-checked and dated (Herries and Adams 2013).

While there is broad agreement in terms of the relative ages of the more prolific faunal assemblages at certain sites, there is far less so when it comes to the chronometric ages of individual faunas (Hendey 1974). Oftentimes these faunas are found well out of their original sedimentary context, and later exposed by wind deflation (Carrión *et al.* 2000) making their original state very difficult to specify (appendix A). Similarly, fossils have regularly been collected in an unsystematic way,

making spatial relationships and associations impossible to ascertain (Klein 1988). Moreover, it is common custom for palaeontologists to infer the ages of fossils based on dates obtained from surrounding sediment. This could lead to inaccuracies due to fossils shifting out of their original context.

A further setback in attempting to date these sites is that the depositional aspects and stratigraphy are not well understood, so it becomes increasingly difficult to establish an accurate sequence of events (Jacobs *et al.* 2008). Fossil assemblages are often subject to time-averaging, greatly diminishing overall temporal resolution (Fig. 2.4.2). Additionally, much of the material from these deposits are now so far removed from their original context to accurately determine their stratigraphic association (Rightmire 1975). Well known assemblages are sometimes local in space but not in time; where fossils from a single locality may have been accumulated across a long period of time (Hendey 1974). This oftentimes leads to assumptions of co-occurrence. Taxonomy at the species level should, logically, be consistent with stratigraphic conclusions, and accordingly the relationships between fossil animals can only be recognised within a well understood stratigraphic framework (Bell 1950). The incompleteness of the fossil record, however, is less of an issue than the adequacy of the data that is present for testing hypotheses around species discrimination (Kidwell and Flessa 1995). Assuming that stratigraphic sequences in faunal assemblages may only be taken as species that succeed each other in time is dangerous, as Bell (1950) notes:

"There is no widely accepted belief in geology that so stultifies paleontologic interpretation as does the belief that successive faunal assemblages in a succession of rocks can be interpreted only as comprising species that succeed each other in time. They may be so interpreted, especially if they are separated by hiatuses, but within

a succession of conformable sediments, particularly if the sediments represent significantly different depositional environments, a more likely interpretation is that the vertically disposed "species" actually are ecologically segregated subspecies" (Bell 1950: 493).

Interpreting stratigraphy in only this way can result in a lack of consideration for other possibilities related to faunal occurrence, species turnover and issues of taxonomic relatedness between the species present. As discussed above, historically, species naming in palaeontology has primarily been concerned with searching for differences rather than similarities. These differences, though,

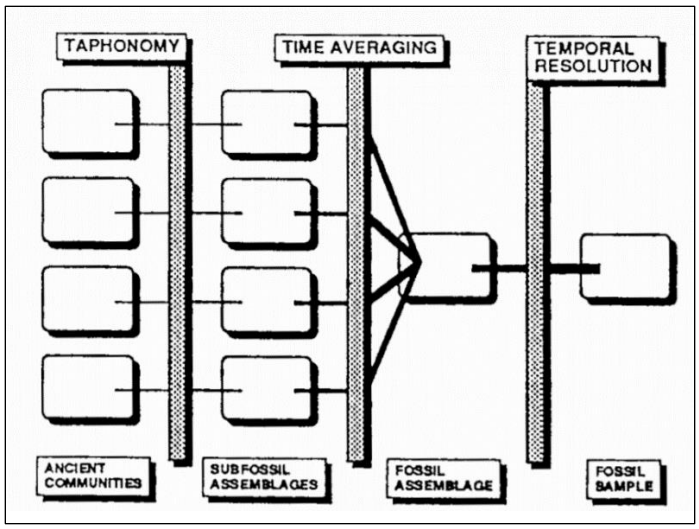



**Figure 2.4.2** The importance of aspects such taphonomy, time-averaging, and temporal resolution in the interpretation of ancient, time-averaged fossil community assemblages. The weight of the branching lines connecting the boxes illustrates the confidence of palaeoecologists in their interpretation once the fossils have been affected by aspects such as time averaging and taphonomy (Kaesler 1991).

are between populations of animals and are based on the comparative anatomy of (usually) incomplete fossils (Bell 1950). This is where the importance of accurate stratigraphy comes in. Modern taxonomy and genetics have justified the hypothesis that states morphological differences

are often an expression of genetic differences, but issues arise due to lack of instruction or guidance in evaluating those differences taxonomically when working solely with fossil remains (Bell 1950). However, if conclusions can be reached on the distribution in time and space of the morphologically distinguishable populations, there exists a guide for approximating genetic affinity. In attempting to do this, depositional knowledge of the populations in time and space can indicate whether morphological difference is the result of two contemporaneous populations, or populations that are separated from each other in time (Bell 1950). Simply contrasting anatomical differences – as has been done with *E. capensis* and *E. quagga* due to a lack of clarity on the timing of each other's deposition – cannot accurately solve this problem.

### 2.5 Using Dental Morphology to Investigate the Taxonomic Distinctiveness of *E. capensis*

Teeth are useful for palaeontological research for a host of reasons, due to the array of unique qualities that they possess (Scott and Turner 1988). Enamel is hard, and therefore preserves in relative abundance. Mammalian teeth have been used extensively for studying the interrelationships of growth, evolution and function (Fortelius 1985). Fossil teeth have been a vital source of information for analyses of genetic compositions, health, diet, behavioural differences and evolutionary relationships (Savara 1965, Scott and Turner 1988). It is known that a biological trait is only useful for historical-evolutionary examination if a significant element of its variation is determined by genetics (Scott and Turner 1988), which is the case with dentition. It has also historically been more difficult to interpret general tooth size than differences in crown morphology (Scott and Turner 1988). There can be much variation in general size, suggesting that size is in fact more responsive to factors like environmental changes and selection, than morphology. Nutrition (and by extension environmental factors) evidently plays a crucial role in

the size and morphological development of teeth, therefore they serve as useful samples in assessing biological relationships and trends of microevolution (Scott and Turner 1988).

Mammalian teeth are composed of four dental tissue types, each of which has its own advantages for analyses (except in the case of pulp which is a non-mineralized tissue). Enamel is the densest, hardest and least porous of the tissues, therefore making it the most durable and the key element in allowing teeth to preserve for so long in the fossil record. It is often the enamel tooth crowns that survive where all other traces of a skeleton are obliterated by chemical or microbial attack (Kendall *et al.* 2018). Added to this, the enamel structure is a record of the tooth's growth, so it is the structure as well as the cell movement patterns that are able to be studied, and by extension the changes in these patterns followed through phylogeny (Fortelius 1985). Enamel shows that the evolution of morphology is the evolution of ontogenetic developments. Dentine is valuable for archaeological study as it preserves well in the fossil record. The diameter of its porosity is smaller than that found in bone, and the tissue does not connect with the exterior of the skeletal element (Kendall *et al.* 2018). This is essentially what makes the tooth the best part of the skeleton to study. The fine composition of these dental tissues affects the mechanical properties of teeth, as well as directly reflecting the developmental processes (Fortelius 1985). There are relationships between evolution, morphology and function. Horse teeth in particular preserve incredibly well as fossils, and are taxonomically easy to identify due to their morphological markers in occlusal surface enamel patterns (MacFadden 2005a, Seetah *et al.* 2014).

Mammalian tooth morphology has been extensively compared and described, documenting tooth evolution (Creighton 1980, Fortelius 1985) through comparisons of relative sizes, shapes and

positions of crests and cusps. Classification of mammalian teeth is of great value in determining mammal phylogenies. As Gould (2002: 96) so eloquently states: “mammalian evolution is the interbreeding of two sets of teeth to produce some slightly modified descendent choppers”. The importance of dentition in studies of variability between and within species is clear due to tooth survival through time, and by extension its frequent recovery in excavations (Scott 2008). Recognizing two species from one another is far less challenging when there are apparent morphological differences distinguishing them, but those that are close or even conspecific in relation are often indivisible on form alone, known to differ only in terms of size (Gingerich 1974). Teeth are defined by ample genetically determined traits, are adaptable while at the same time evolutionarily conservative, and have relative durability and internal complexity (Savara 1965, Scott and Turner 1988, Scott 2008).

Analysis of dentition in archaeological and palaeontological studies has been indispensable for establishing taxonomies affiliations and feeding behaviours in fossil taxa. Teeth oftentimes fill gaps in the fossil record due to the degradation of the target species’ DNA, bones and other morphological materials. As such, teeth are ideal for evaluating the contesting ideas of the taxonomic status of *Equus capensis*.

### 2.5.1 Morphometric Approaches for Species Discrimination

Taxonomists use morphological differences to define and differentiate between and amongst species, and teeth allow for this type of examination in their varied enamel patterns. It is thought that variation of morphology is categorized by gaps between taxa (MacLeod 2002), and shown that morphometric approaches have a much higher accuracy than the more subjective visual

methods for the identification of morphologically ambiguous species (Mutanen and Pretorius 2007). The latter methods are not in accordance with "scientifically logical principles" (Mutanen and Pretorius (2007: 381). One example of the inaccuracy of visual interpretation is case of *Equus capensis* (Fig. 2.2.1), with Cooke (1950) and Broom (1928) illustrating the same type specimen in vastly different ways from one another. Geometric methods offer an effective and unbiased means for the demarcation of species, and pinpoint even the smallest morphological differences for the species-level taxonomist.

Teeth do not remodel once formed, and, once developed, they do not change throughout the animal's life (Gingerich 1974, Cucchi *et al.* 2017). Consequently, enamel patterns of cheek teeth are popular amongst palaeontologists for taxonomic identifications, and are particularly valuable for reconstructing phylogenies of extinct taxa (Cucchi *et al*. 2017). Developments in fields of morphometrics have made it possible to graphically visualize and statistically clarify complex occlusal tooth patterns such as those seen in equids, and has proven to be effective in distinguishing between equid species.

In attempts to determine taxonomies, it is also vital to reconstruct past environmental conditions that may have influenced the evolution of Ungulata (Kaiser and Solounias 2003). While extant equids typically consume large quantities of grass (Nowak 1991), they are able to vary their diets according to their environment and food availability (Schulz and Kaiser 2012). For example, a mesowear analysis of *Equus quagga* from seven different African habitats found a high level of dietary variation (Kaiser and Schulz 2006). In a follow-up study, Schulz and Kaiser (2012) conducted a mesowear analysis of nine extant equid species. The results supported their hypothesis

that local climatic conditions determined feeding behaviour. Thus, while the range of dietary behaviours in modern equids has traditionally been presented as narrow (where all equids are stated to be grazers), these results show that the dietary traits of modern *Equus* are more diverse than previously acknowledged. This appears to specifically be the case in *E. quagga*. Additionally, Viranta and Mannermaa (2014) conducted mesowear analysis on Finnish medieval horses and compared their results to those from Estonian medieval horses. The results differed across the regions, with a more graze-dominated signature in Estonian horses and Finnish horses preferring browse. This dissimilarity in dietary preferences between localities is comparable to the mesowear profiles obtained for modern zebras (Fortelius and Solounias 2000) versus the *Equus capensis* samples from Kaiser and Franz-Odendaal (2004)'s study. Dietary flexibility appears to have been present in Pleistocene equid populations as well. It is evident that further exploration on *E. capensis* is needed to conclusively validate its dietary preference.

As mentioned, dental occlusal form and enamel folding patterns carry taxonomic information in equids (Mutanen and Pretorius 2007, Seetah *et al.* 2014, Cucchi *et al.* 2017), and thus can inform on the taxonomic status of *E. capensis*. What follows is the first quantitative analysis of these features, attempting to shed light on where the large zebra belongs within equid phylogeny. Landmark data were used to analyze enamel folding patterns via geometric morphometrics, and traditional linear measurements were used to evaluate overall dental occlusal form. The complexity of occlusal enamel folding patterns is indicative of what an animal is genetically predisposed to eating, and this was investigated using occlusal enamel index analysis. Finally, dental mesowear variables were recorded, and mesowear analysis was carried out to investigate the dietary behaviour of *E. capensis*.

# Chapter Three

## Materials and Methods

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### 3.1 Materials

The material analysed in this study consists of fossil and extant *Equus* upper and lower molar and premolar teeth, curated in South African museum and university collections (Table 3.1). The fossil sample is diverse, consisting of teeth from 19 South African archaeological/palaeontological locations. The extant sample used for comparative purposes in this study was derived from 4 species – *Equus caballus*, *Equus quagga*, *Equus zebra* and *Equus asinus*. Lastly, measurements from a small sample of *Equus* dental material from East Africa were also incorporated into my analyses for the purpose of comparison. These were derived from scaled images of teeth from *Equus quagga*, *Equus grevyi*, *Equus oldowayensis* and an equid with affinities to *E. capensis,* all of which were supplied by Dr. Tyler Faith. It must be noted that for all samples analyzed, their literal taxonomic identification was used. Accordingly, when a box or individual specimen within the collections was labelled '*Equus capensis*', I classified it as such. The same was the case for all other species delineations included in the research.

Members of the genus *Equus* have three premolar (P2/p2, P3/p3, P4/p4) and three molar teeth (M1/m1, M2/m2, M3/m3) (Fig. 3.1.1). Premolars and molars carry taxonomic information and were therefore the focus of this study. With the exception of the second premolar and the third molar, mandibular premolars and molars are difficult to tell apart from each other, and the same goes for maxillary premolars and molars. This is problematic since *Equus* teeth are almost always

found in isolation in archaeological/palaeontological contexts. To facilitate analyses, third premolars, fourth premolars, first molars and second molars were lumped together and analysed as a single tooth type. Previous studies have found that this approach does not significantly alter

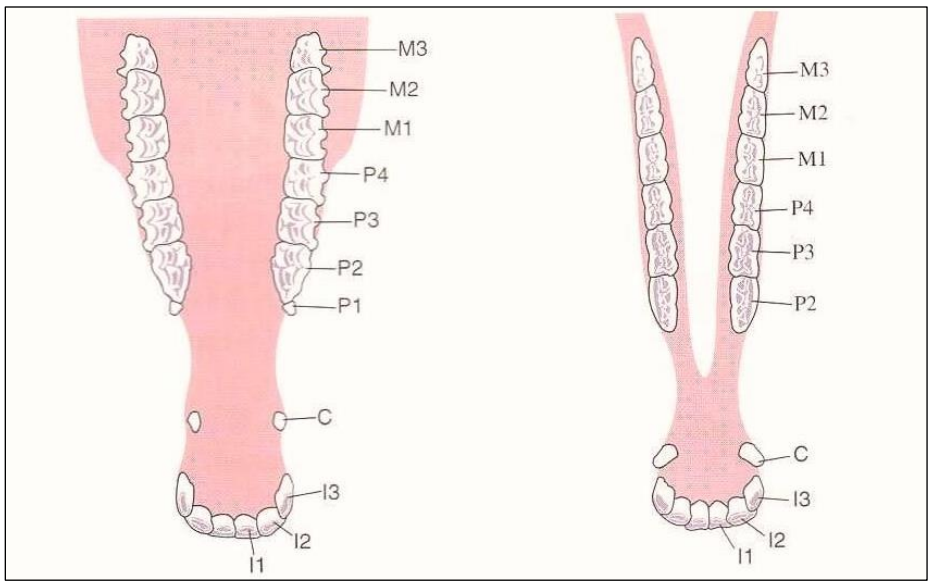


**Figure 3.1.1** Aerial view of the upper (left) and lower (right) jaws of *Equus*, showing positions of all premolars and molars (Björnsdóttir 2019).

results as they are not significantly different from one another, and may be used interchangeably in broad level analyses such as this (Famoso and Davis 2014). In cases where teeth were part of tooth rows, a single tooth was recorded. For consistency sake, the p4 was the chosen tooth (where possible) for mandibular teeth, and the M2 (where possible) for maxillary teeth. These two tooth types were generally the most abundant as well as the best preserved in the studied sample. The P2/p2 and M3/m3 were not analysed, as these teeth differ significantly in shape from the middle four, and their inclusion in analyses would lead to skewing of results. It has been determined that age and wear do not distort taxonomic information or centroid size in equid teeth (Seetah *et al.* 2014), however all juvenile and overtly worn teeth were excluded.

**Table 3.1** The total number of specimens used from both upper and lower jaws, indicating the sites from which the samples came and the institutions in which the specimens are held.

| Site | # *E. capensis* | # *E. quagga* | # other *Equus* | Curated |
|---|---|---|---|---|
| **Elands Bay Cave** | 4 | 0 | 0 | Iziko South African museum |
| **Elandsfontein** | 41 | 0 | 38 | Iziko South African museum/UCT |
| **Boomplaas** | 7 | 0 | 5 | Iziko South African museum |
| **Nelson Bay Cave** | 0 | 2 | 0 | Iziko South African museum |
| **Byneskranskop** | 1 | 1 | 1 | Iziko South African museum |
| **Vlakraal** | 0 | 0 | 40 | Florisbad Quaternary Research Station |
| **Florisbad** | 0 | 0 | 76 | Florisbad Quaternary Research Station |
| **Spitskop** | 9 | 0 | 0 | Florisbad Quaternary Research Station |
| **Equus Cave** | 0 | 0 | 128 | Florisbad Quaternary Research Station |
| **Calvinia** | 0 | 0 | 1 | Florisbad Quaternary Research Station |
| **Sand River** | 0 | 0 | 2 | Florisbad Quaternary Research Station |
| **Mahemspan** | 0 | 0 | 19 | University of the Witwatersrand |
| **Cave of Hearths/ Makapansgat*** | 17 | 21 | 19 | University of the Witwatersrand |
| **Buffalo Cave** | 0 | 0 | 1 | University of the Witwatersrand |
| **Coopers Cave** | 2 | 0 | 0 | University of the Witwatersrand |
| **Kalkbank** | 15 | 27 | 5 | University of the Witwatersrand |
| **Swartkrans** | 5 | 0 | 0 | University of the Witwatersrand |
| **Plovers Lake** | 0 | 4 | 0 | University of the Witwatersrand |
| **Gladysvale** | 9 | 0 | 1 | University of the Witwatersrand |
| **Olorgesailie** | 0 | 0 | 3 | National Museums of Kenya |
| **Amboseli** | 0 | 0 | 2 | National Museums of Kenya |
| **Kisaaka** | 0 | 2 | 3 | National Museums of Kenya |
| **Onge** | 0 | 1 | 0 | National Museums of Kenya |
| **(Modern samples)** | N/A | N/A | 28 | University of Cape Town |
| **Total** | **110** | **58** | **372** | |

*composite sample.

## 3.2 Methods

Landmark data, and measurements required to calculate the occlusal enamel index, were generated from photographs of occlusal surfaces. For linear measurements and mesowear analysis, teeth were measured directly. Photographs were taken of specimens with well-preserved occlusal surfaces (Fig. 3.2.1). Each photograph included a 15cm scale bar at the height of the occlusal

surface and the specimen number. The scale was raised using putty to make it level with the occlusal surface of the teeth. The teeth themselves were straightened and leveled also using putty, ensuring that the camera lens faced the occlusal surface head on and was parallel to the focal place of the camera's lens. All photographs were taken with a Nikon D5100, 16.2-megapixel digital camera, and were taken away from direct light to avoid shadows. The total number of teeth used for analysis differs between the four methods, as well as the division of upper and lower teeth (Table 3.2). The reason for this is that each method requires a particular state of preservation for analysis, so not all teeth were viable for each analysis (appendix F).

Lastly, the specimens were not assigned to sex. While there are some size differences between male and female equids, there is in fact large overlap between the sexes (Van Asperen 2013). Extant male equids are roughly only 10% larger than females (Estes 1991), and zebras in particular are noted as having body sizes that are virtually identical between sexes (Neuhaus and Ruckstuhl 2002). Known to live in social groups, a lack of sexual dimorphism in zebras is explained as a need to coordinate feeding and movement behaviours with other group members, thus allowing them to live in stable bands (Neuhaus and Ruckstuhl 2002). Modern *Equus quagga* in particular is a species that illustrates no significant sexual dimorphism in overall body mass, with females weighing roughly 220kg and males only slightly more at about 250kg (Estes 1991, Neuhaus and Ruckstuhl 2002). Seetah *et al.* (2014) also evaluated the use of morphometrics in occlusal enamel patterns to determine differences between horse populations in terms of sexual dimorphism, age (or wear) and allometry. It is known that male equids have spade shaped canines that are used for fighting, while females do not (Estes 1991), but little in the way of dimorphism has been recognised beyond this. It was found that there is no meaningful sexual dimorphism in the size and

shape of cheek teeth (Seetah *et al.* 2014), and it, along with wear, does not complicate discernment of equid populations, proving the potential for exploring matters of taxonomy in ancient equids using dentition morphometrics. Outside of this, sexual dimorphism is anyway not expected to affect equid dentition size, as even mammals that are extremely sexually dimorphic are not known to have significant differences in overall tooth size (Van Asperen 2013).

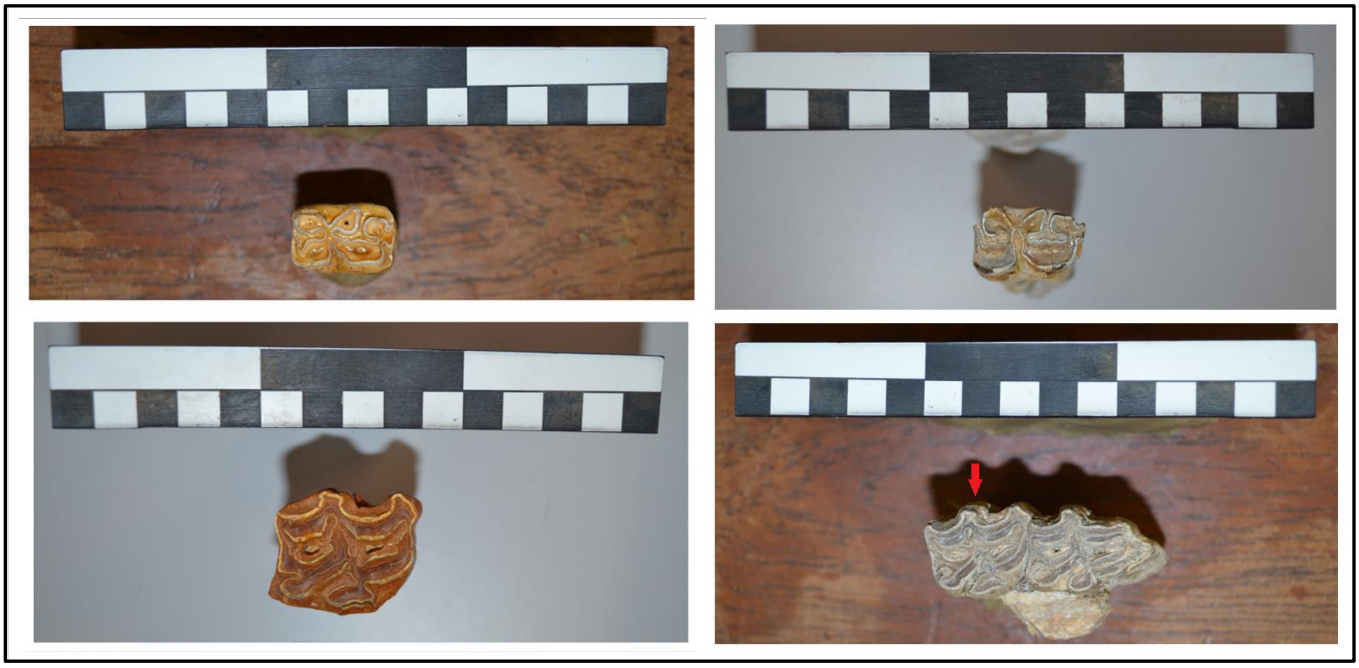

**Figure 3.2.1** Examples of the photographs of equid specimens used for geometric morphometric and occlusal enamel complexity analysis. Top mandibular: Left = *Equus quagga* from Cave of Hearths (COH28-30); right = *Equus capensis* from Elandsfontein (Q34A). Bottom maxillary: Right = *Equus quagga* from Kalkbank (323); left = *Equus capensis* from Elandsfontein (2499A).

**Table 3.2** The number of specimens used for each method employed and the associated jaw which the specimens come from.

| | Mandible | Maxilla | Total |
|---|---|---|---|
| **No. of Specimens for GMM** | 181 | 255 | **436** |
| **No. of Specimens for Linear Measurements** | 214 | 322 | **536** |
| **No. of Specimens for Mesowear** | 0 | 123 | **123** |
| **No. of Specimens for OEI** | 0 | 128 | **128** |

### 3.2.1 Linear Measurements

Traditional linear distance measurements of dental occlusal surfaces were recorded for all analysed dentition (Fig. 3.2.2). The method for measuring equid bones and teeth introduced by von den Driesch (1976) was employed, as the methods in the compilation have served as a standard from which scholars have continued to refer. Digital calipers were utilized for measurement to record maximum length and breadth measurements in millimeters, correct to two decimal places (appendix B). While tooth breadth is supposedly a more accurate proxy for body size than length (Albarella *et al.* 2005), to better clarify the overall size and proportions of an animal it is better to record more than one dimension. For this reason, length measurements were included as well. The size of the limbs and dentition of *Equus capensis* have previously been emphasized as important factors in classifying the species, therefore this element of assessment (wholly separate from the other three methods of analysis, and the only one to be implemented on every tooth) adds an important and necessary dimension to the research. Principal components (PCs) were generated on Past 3 (Hammer *et al*. 2001) from the length and breadth measurements and the first two PCs were plotted against each other to visually compare differences in occlusal form across samples. One-tailed t-tests were run on principal components to test for any significant differences between samples.

### 3.2.2 Geometric Morphometrics – Thin Plate Splines

Geometric morphometrics (GMM) is the statistical analysis of shape variation, and its correlated variation with other elements. Landmark-based GMM provides a robust approach for the quantification of shape, shape variation, and covariation of shape in biology (Webster and Sheets

2010, Zelditch *et al.* 2018). The method quantifies differences in the shapes of anatomical objects using the Cartesian coordinates of previously determined anatomical landmarks (Adams *et al.* 2013). Landmarks are chosen points that are physically and biologically comparable as well as

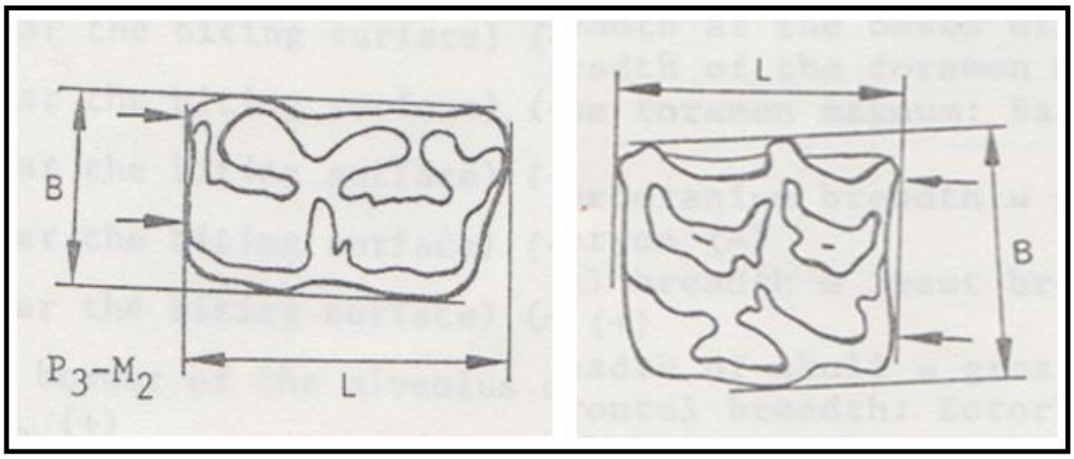


**Figure 3.2.2** *Equus* mandibular (left) and maxillary (right) tooth, length (L) and breadth (B) at the biting surface (von den Driesch 1976). Both illustrations are expressions of P3 – M2 and exclude M3 and P2.

identifiable on all organisms being examined, and are in homologous positions on each sample (Webster and Sheets 2010). Degrees of similarities between shapes, as well as similarity/difference in the ontogenetic or evolutionary trajectories amongst species, can be significantly measured through this method (Mitteroecker and Gunz 2009). The detail of the geometric shape variation that the method produces also does more to strengthen the statistical power of the results obtained (Parés-Casanova and Martínez 2013, Zelditch *et al.* 2018).

Many morphological features are often quantified by measurements of their size; however some features are more complex and thus cannot be considered solely based on size (Klingenberg 2010). GMM is ideal for these features, as it considers solely shape information, theoretically defined as

all geometric features of an object apart from the size, position and orientation (Mitteroecker and Gunz 2009). By removing size, position and orientation one is able to clearly delineate the shape differences between specimens. An added advantage to applying this definition of shape, is that overall visualization of the objects becomes simpler in the analyses (Klingenberg 2013), showing only the differences in the specimens' forms. A set of landmarks that represent specific anatomical attributes (Adams *et al.* 2013, Zelditch *et al.* 2018) are acquired. These fixed landmarks are used in the method where they, together with the abovementioned definition of shape, are able to use the shape average (Fig. 3.2.3) in order to distinguish variation around this mean (Bookstein 1996). Added to this, GMM methods overcome the issue of general orientation in isolated teeth (Martinón-Torres *et al.* 2006).

While GMM analyses are typically performed on specific anatomical locations that can be landmarked, the shape of other anatomical features with less obviously clear or fixed positions may also be of interest, as is the case in this study. Curve boundaries are a typical example of this kind of feature. Curves within anatomical features are oftentimes essential to answer particular research questions that attain to variation in these areas, and traditional landmark data is unable to analyze the shape variation that exists as arcs or curves between those landmarks (Webster and Sheets 2010). It is within these types of studies that semi-landmarks can be added to the method, and it is the combination of these landmark types that leads to more comprehensive quantification of shape as well as distinction of taxa (Adams *et al.* 2004). New evidence about biological shape is acquired with this incorporation, therefore different results may be yielded in cases where traditional landmarks have not differed or shown any variation (Perez *et al.* 2006). From one point to the next, connections between similarly shaped curves are gained with the use of semi-

landmarks. This allows for the discrimination of group differences, as these forms would not have clear-cut landmark locations, yet are by no means indistinct (Bookstein 1997). An example is that of the enamel folding patterns on occlusal surfaces of teeth, as they contain smooth outlines that

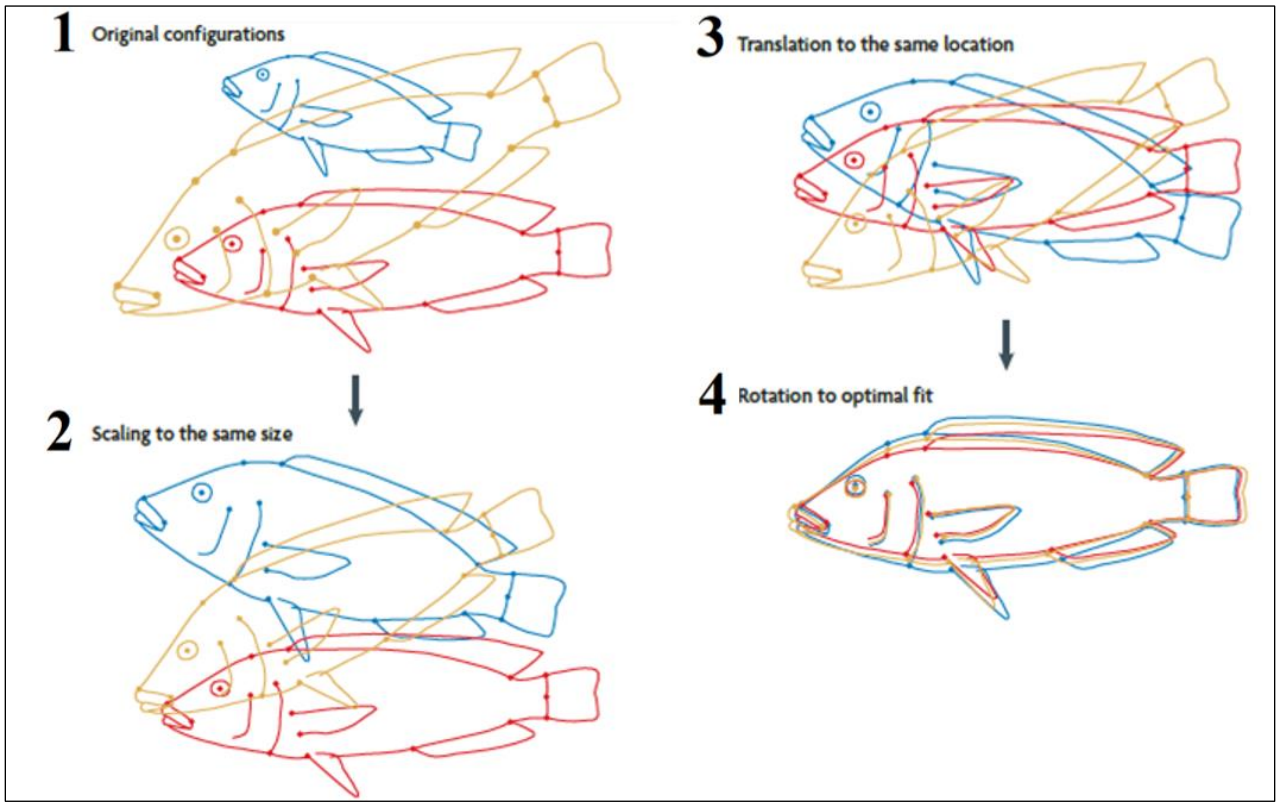


**Figure 3.2.3** Extracting shape information for all specimens in analysis – starting with scaling to the same generic size, then to the same location in space and finally oriented the same way. The variation in the coordinates after the removal of this information is therefore the true variation in shape between specimens (Klingenberg 2010).

are difficult to represent via landmarks. Understandably, the positions of landmarks along a bend will not be analogous across different specimens (Gunz and Mitteroecker 2013).

In terms of GMM in dental studies, sliding semi-landmarks are ideal for analysis of shape variation amongst both different and extremely similar tooth types, as most of this variation exists in the

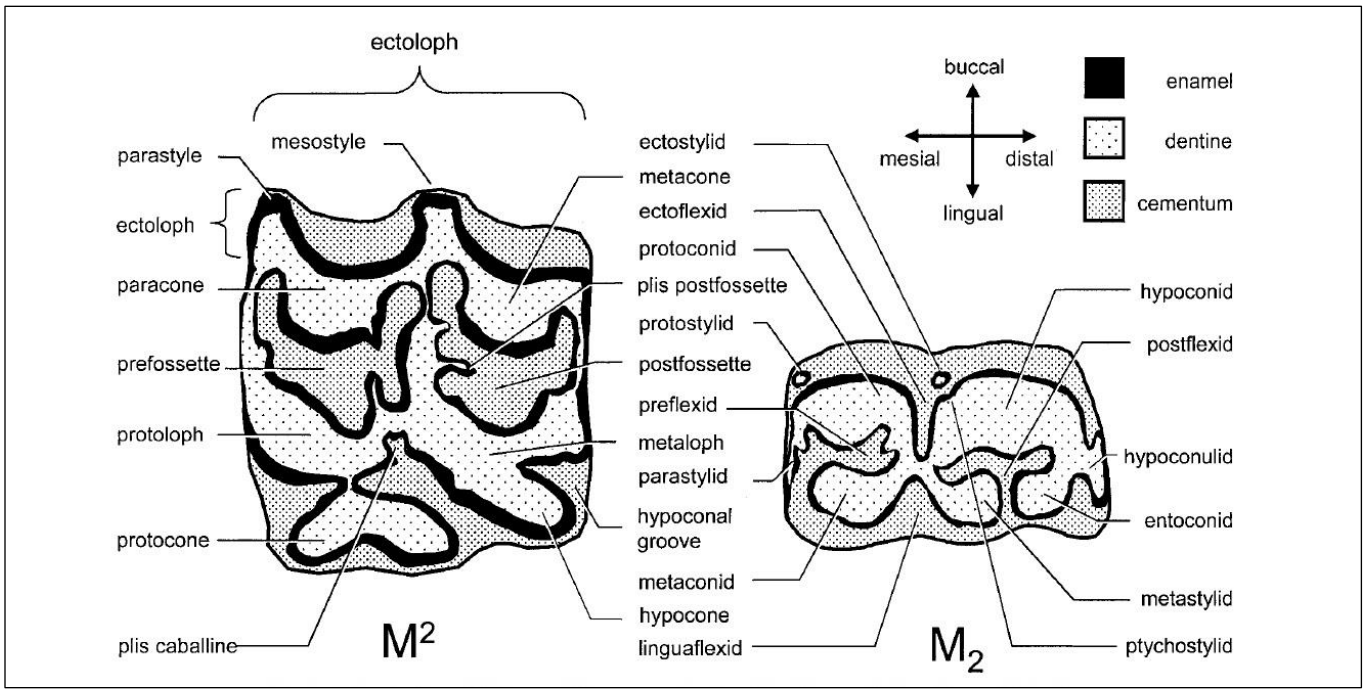


**Figure 3.2.4** Worn occlusal surfaces of upper and lower equid molars and the terminology of their features (Kaiser and Fortelius 2003).

forms of sweeps and curves. Particularly in the case of occlusal morphology, and even more specifically the enamel folding on occlusal surfaces of all equid species, these exteriors consist of many curves (Fig. 3.2.4). Hence, the abovementioned fixed landmarks employed for these types of studies may not yield comprehensive enough results.

Two-dimensional (2D) thin plate splines (TPS) relative warp analyses are amongst the most powerful interpolative methods in morphometrics, used to assign semi-landmarks between curves

of variable but similar shapes (Bookstein 1997, Klingenberg 2013). TPS is solely based on geometric criteria (Klingenberg 2013), and is specifically suited for quantitative group comparisons (Bookstein 1997). Relative warps analyses provide fine scale size and shape differentiation across regional as well as temporal contexts (Ottoni *et al.* 2012). It also analyses the occlusal surface whereas traditional measurements examine overall length and breadth, further broadening the scope of the analysis. The shape captures the most complex parts of equids' enamel folding, so as much biological information as possible is recorded.

Traditional GMM landmarks as well as sliding semi-landmarks were digitized off the photographs (Zelditch *et al.* 2018), and used for analysis. For the lower premolars and molars (p3 – m2), the patterns of the occlusal enamel were recorded using the protocol set forth by Cucchi *et al.* (2017). This approach uses eight landmarks and eight curves, with the same set number of semi-landmarks

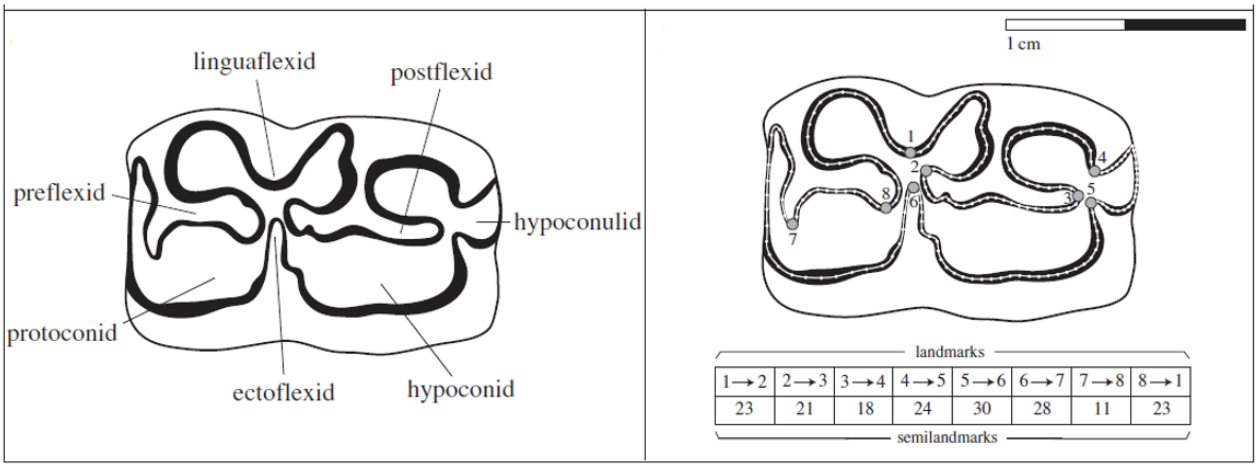


**Figure 3.2.5** Mandibular occlusal surface with the anatomical terminology (left) their GMM protocol (right) for the quantification of the enamel folding with the location of the 8 landmarks (dots with grey filling) and the number of semi-landmarks (table) sampling the curves of the enamel folds between each landmark (adapted from Cucchi *et al.* 2017).

within each curve for each specimen (Fig. 3.2.5). In terms of the mandibular TPS analysis, the only discrepancy between this study and that of Cucchi *et al*. (2017) is that while they ensured the spaces between each semi-landmark were equidistant, this study did not. The reason for this is that, upon close examination of the occlusal patterns, it appeared that the curve could be much more accurately captured when more semi-landmarks were placed in areas of greater curvature, and less were placed in areas with straighter patterning. Rather than adding more semi-landmarks and by extension not following the Cucchi *et al.* (2017) protocol, adjusting the distance between semi-landmarks proved to be an effective solution. Protocol for landmarks with sliding semi-landmarks of the upper premolars and molars (P3 – M2) has yet to be done, and this study presents a novel approach that is based on that of the Cucchi *et al*. (2017) mandibular procedure (Fig. 3.2.6). All landmarks for both the upper and lower teeth were placed on recognizable and homologous

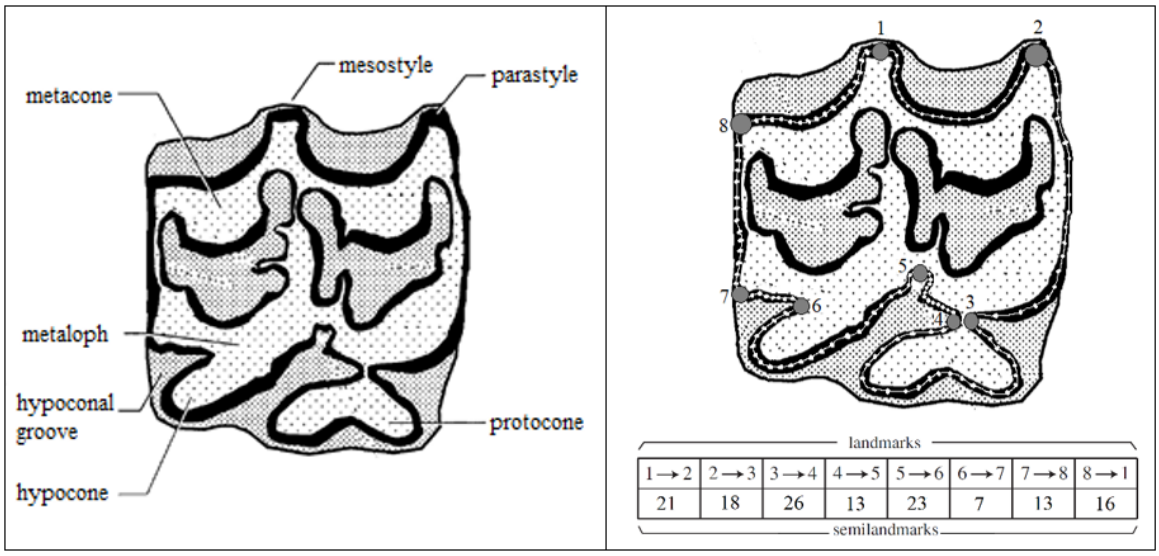


**Figure 3.2.6** Maxillary occlusal surface with the anatomical terminology (left) their GMM protocol (right) for the quantification of the enamel folding with the location of the 8 landmarks (dots with grey filling) and the number of semi-landmarks (table) sampling the curves of the enamel folds between each landmark (adapted after Kaiser and Fortelius 2003).

loci on each specimen, and curves have all been drawn in the centre of the tooth's enamel thickness (Webster and Sheets 2010). All right maxillary teeth were used, and all left mandibular teeth. All images of left maxillas were mirrored right, and all images of right mandibles were mirrored left. All digitization of images (landmarks and semi-landmarks) were performed on TPSDig v.232 (Rohlf 2006). Scaling of all images was also performed using TPSDig v.232, and a new scale factor was set for each individual image, due to the fact that the images were not photographed at exactly the same magnification or at the same distance from the camera's lens (Zelditch *et al.* 2018), so the number of pixels per mm varied very slightly from photograph to photograph. Therefore, an individual scale factor for each image ensured accurate centroid size calculation. The 15cm scale bar was used for creating the scale factor, and where no ruler existed (such as in images supplied to me and not photographed by myself), the length across the occlusal tooth surface (supplied by the photographer) was used to set the scale factor. Before semi-landmark superimposition was possible, the control lines distinguishing curves from traditional landmarks had to be removed. TPSUtil v.64 (Rohlf 2005a) was used to remove these control lines, as this program detects possible mistakes that may have occurred whilst digitizing the images in TPSDig v.232. It was consequently ensured that all images contained the same number of landmarks and semi-landmarks, and that they were all placed in the correct order. Once all mistakes were identified and corrected, the TPS curves were appended to landmarks and the edited file was saved. A 'sliders file' was then prepared in TPSUtil v.64 to indicate which points were semi-landmarks and which points they slid between. This file, together with the original TPSDig v.323 file of appended landmarks, was then able to be run in TPSRelw v.32 (Rohlf 2005b) for semi-landmark superimposition. All of the abovementioned steps were performed separately for both the mandibular and maxillary teeth.

In order to analyze the occlusal enamel shape of teeth, information related to size, position and orientation were removed via a Generalized Procrustes Analysis (GPA) (Gunz and Mitteroecker 2013) that was run using TPSRelw v.32. This aligns the landmark coordinates using a least squared approach. In contrast to traditional landmarks, sliding semi-landmarks are not positioned in anatomically recognizable and distinct loci along the enamel and, therefore, during GPA superimposition, they are slid along the lines of the curves using bending energy (Bookstein 1997) to minimize shape configuration differences. The result of the GPA is a new set of superimposed coordinates that can be analysed and classified as shape coordinates independent of the abovementioned factors known to distort shape configurations. Centroid size, a proxy for size, was also calculated using this superimposition. Partial Warps and Relative Warps scores (proxies for shape) were then calculated on the set of coordinates. The Relative Warps in TPSRelw v.32 are similar to Principal Component (PC) scores (Zelditch *et al.* 2018), and these scores were saved along with the centroid sizes (appendix C). A range of statistical tests were performed on the centroid sizes (ANOVA, Mann–Whitney, Kolmogorov Smirnov, Levene's) as well as the first five PC scores (MANOVA, Wilk's Lambda, Pillai trace) to test for significant size/shape differences between samples. All statistical tests were run in Past 3 (Hammer *et al.* 2001). Centroid sizes and PC scores were also plotted in scatter plots to visualize differences in size/shape between samples.

### 3.2.3 Occlusal Enamel Index

There is a clear relationship between dental function and enamel structure (Maas 1991), with enamel organization adaptively related to masticatory stress on the teeth. This organization contains an explicit signal of adaptation (Rensberger 2000, Lucas *et al.* 2008). Therefore, the form

of the enamel allows one to make inferences about behaviour in the diets of extinct species such as *E. capensis*. This type of analysis is beneficial to conduct in conjunction with the mesowear method discussed below, since mesowear reveals the types of vegetation that species were eating, and occlusal enamel index (OEI) is a morphological signal denoting what they are adapted to eating. OEI responds to changing feedings strategies, where an increasingly grass-dominated diet, as was the case for most herbivores living through the Pleistocene-to-Holocene transition, results in an increased OEI (Famoso *et al.* 2013, Famoso *et al.* 2016). Added to this, relative enamel complexity between clades is also influenced by phylogenetic relationships (Famoso and Davis 2014) and is therefore a good tool for evaluating evolutionary relationships within and between taxa.

A total of 68 of the recorded specimens were included in the OEI analysis, 39 of which have been classified as *E. capensis*, and 29 as *E. quagga*. These specimens come from a variety of southern African sites. Maxillary teeth were used because prior studies of equid OEI have utilized upper rather than lower teeth (Famoso *et al.* 2013, Famoso and Davis 2014). It has been determined that P3 – M2 do not differ significantly in the OEI of upper teeth, thus those used in this study were a combination of the upper middle four teeth. While it is true that premolars may be larger than molars, size variation within a given population overpowers this difference in size when it comes to isolated teeth (Famoso and Davis 2014). To quantitatively measure and test differences in enamel complexity across species, Famoso *et al.* (2013) introduced the Occlusal Enamel Index (OEI): = OEL/√(True Area). Occlusal Enamel Length (OEL) is the total length of enamel exposed on the tooth's surface, and true area is the total occlusal surface area that follows the outer edges of the occlusal surface and including any cementum that may exist outside of the enamel, though

on the lingual side only and not the buccal (Fig. 3.2.7) (Famoso and Davis 2014). OEL as well as true occlusal tooth area were measured for each specimen on the digitally photographed images (appendix D). OEI is imperative for this type of analysis, as those teeth classified as *E. capensis* are expected to produce greater occlusal enamel lengths than *E. quagga* due to their significantly larger general size, and since true area is a proxy for general body size, OEI removes the effects that absolute scale would have on the complexity of the respective species. The enamel measurements were performed using the public domain NIH image program ImageJ (Schneider *et*

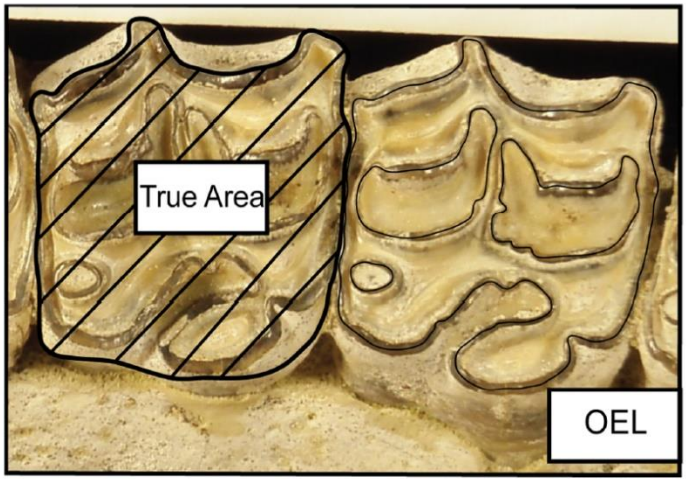


**Figure 3.2.7** Examples of true area and occlusal enamel length (OEL) measurements taken on digital images of equid upper dentition, calculated with ImageJ (Famoso and Davis 2014).

*al*. 2012), and all images were scaled individually using the same program. Statistical tests (Mann–Whitney, Kolmogorov Smirnov, Levene's) were run in Past 3 (Hammer *et al*. 2001) on the *E. capensis* and *E. quagga* samples, as well as four other equid species (Table 3.3) with existing OEI scores from Famoso and Davis (2014).

### 3.2.4 Mesowear

Dental mesowear is a dietary reconstruction technique that involves the assessment of facet

**Table 3.3** Equid species included in occlusal enamel complexity analysis and number of maxillary teeth measured for each species.

| Species | # Teeth |
|---|---|
| *Equus capensis* | 39 |
| *Equus quagga* | 29 |
| *Equus quagga* (modern) | 24 |
| *Equus asinus* | 6 |
| *Equus grevyi* | 6 |
| *Equus caballus* | 24 |
| **Total** | **128** |

development on the buccal (lateral) side of ungulate molar occlusal surfaces. It is an effective proxy for the reconstruction of paleodiets in Ungulata due to dental wear patterns being strongly influenced by diet (Rivals *et al.* 2007, Viranta and Mannermaa 2014, Belmaker and O'Brien 2017). While at its inception the method was restricted to upper M2s (Fortelius and Solounias 2000), it has since been extended to include various other cheek teeth as well, making an already powerful analysis – its simplicity and efficiency means thousands of samples can be tested – even more so, as the more tooth positions available for examination, the more reliable the paleodietary examination (Kaiser and Fortelius 2003). This in turn increases the basis for statistical analysis to make dietary reconstruction more significant (Kaiser & Solounias 2003).

When ungulates feed, the degree of facet development on dental occlusal surfaces is determined by a combination of tooth-on-tooth contact (attrition) and food-on-tooth contact, (abrasion) (Kaiser and Schulz 2006, Rivals *et al.* 2007, Viranta and Mannermaa 2014). Attrition creates facets on selenodont teeth, and abrasion eradicates them due to food wearing the enamel tissue down during mastication (Blondel *et al*. 2010). The degree to which either attrition or abrasion affects occlusal

surfaces is determined by the physical properties of plant foods consumed. Plants that are rich in phytoliths, such as monocotyledons, are highly abrasive. Consequently, the teeth of ungulates that primarily consume monocotyledons, typically grazers, are most affected by abrasion. On the other hand, dicotyledonous plants such as shrubs, are less abrasive. The teeth of ungulates that primarily consume dicotyledons, typically browsers, are most affected by attrition (Schulz and Kaiser 2012). Those that are more flexible in their diets are known as mixed-feeders, usually consuming both browse and graze interchangeably and thus showing approximately equal effects of attrition and abrasion.

Equid teeth are ideal for mesowear analysis for a number of reasons. Because equid teeth are hypsodont, they contain flatter ectoloph wear shapes and occlusal surfaces; and the buccal and lingual side are more similarly developed than those of brachydont teeth (Fortelius 1985). The categories for fossil ungulate crown heights are brachydont (low-crowned teeth), hypsodont (high-crowned teeth), and mesodont (medium sized teeth), and these groups are often applied as proxies for the abovementioned key dietary categories (Mihlbachler and Solounias 2006). Although there is a correlation between crown height and environmental factors in modern ungulates, it is not an accurate enough proxy for interpreting diet in terms of browsing versus grazing, thus mesowear is a useful tool to aid in these reconstructions (Mihlbachler and Solounias 2006). The method is ideal for determining a long-term profile for the feeding behaviours of equid species that are absent today. Reasons for this are chiefly due to their dental facet development's strong association with their feeding preference (Blondel *et al.* 2010), as well as the mesowear signature taking months/years to develop (Rivals *et al.* 2007) consequently reflecting diet on an extended scale of time.

All teeth used for mesowear analysis in this study were assessed directly. The two features used for analysis are the occlusal relief and the cusp shape. Occlusal relief, related to the cusp height, was assessed based on how high the cusps appear in lateral view and categorized as either high (h) or low (l) (Fig. 3.2.8). The relief is dependent on how high the cusps rise above the valley between them (Stynder 2009), and because low occlusal relief may also be a result of wear stages, the sharpest of the two buccal cusps (the paracone or the metacone) is scored (Kaiser and Schulz 2006, Blondel *et al.* 2010). An abrasion dominated diet will move the mesowear equilibrium towards

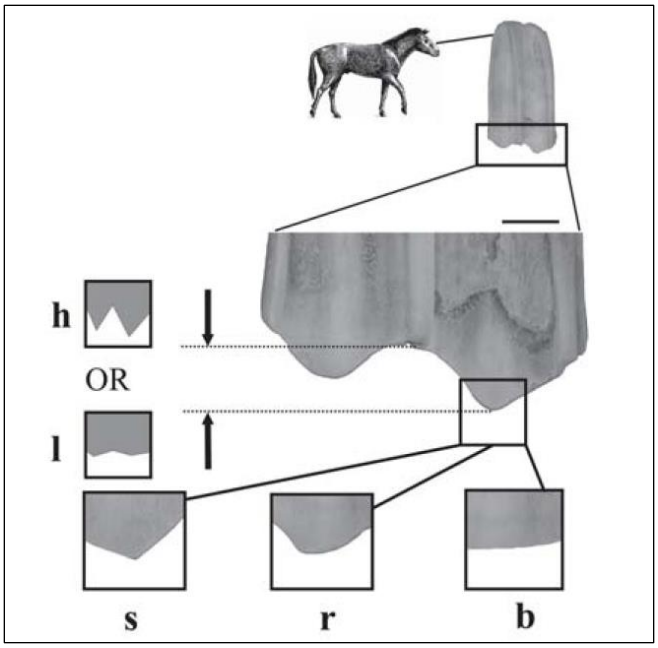


**Figure 3.2.8** Portrayal of how the two mesowear variables are determined for equid teeth. Occlusal relief that focuses on the higher of the two reliefs between each cusp is scored as 'high' (H) or 'low' (L), and cusp shapes focusing only on the sharpest cusp may be scored as 'sharp' (S), 'round' (R) or 'blunt' (B) (Kaiser and Schulz 2006 after Kaiser and Solounias 2003).

round or blunt cusps and low occlusal relief, while attritive diets will result in high occlusal reliefs and sharper cusps (Viranta and Mannermaa 2014, Belmaker and O'Brien 2017). Whether a cusp

was classified as high or low was based on general measurements (high = >1mm, low = <1mm) made on all teeth using a digital caliper, correct to two decimal places in millimeters (appendix E). The percentages of high and low occlusal reliefs were calculated (Table 3.4) and then used as variables in the generation of a hierarchical cluster analysis that classified the samples in the grazer, browser, and mixed feeder categories in relation to 26 extant ungulates with known feeding preferences (Table 3.5). The second feature, cusp shape, is categorized as either sharp (s), round (r) or blunt (b) (Fig. 3.2.8), and similarly to the occlusal relief, both cusps' shapes on the molars were individually identified and the sharper of the two is the classification that was used. If one of the two cusps were broken, the unbroken cusp shape was the one used. If both cusps were broken, the tooth was not included in the analysis. The percentages of sharp, round and flat cusps were then calculated for all specimens (Table 3.4), and also used as variables in a hierarchical cluster analysis.

**Table 3.4** Mesowear scorings of *E. capensis* and *E. quagga* across sites. *n*=number of dental specimens, *l*=absolute scorings of low occlusal relief, *h*=absolute scorings of high occlusal relief, *s*=absolute scorings of sharp cusps, *r*=absolute scorings of round cusps, *b*=absolute scorings of blunt cusps, *%l*=percentage of low occlusal relief, *%h*=percentage of high occlusal relief, *%s*=percentage of sharp cusps, *%r*=percentage of round cusps, *%b*=percentage of blunt cusps (after Fortelius and Solounias 2000).

| **Site & Species** | ***n*** | ***l*** | ***h*** | ***s*** | ***r*** | ***b*** | ***%l*** | ***%h*** | ***%s*** | ***%r*** | **%b** |
|---|---|---|---|---|---|---|---|---|---|---|---|
| **Elands Bay Cave** *E. capensis* | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 100 | 0 | 100 | 0 |
| **Boomplaas** *E. capensis* | 3 | 0 | 3 | 0 | 3 | 0 | 0 | 100 | 0 | 100 | 0 |
| **Elandsfontein** *E. capensis* | 26 | 0 | 26 | 0 | 26 | 0 | 0 | 100 | 0 | 100 | 0 |
| **Nelson Bay Cave** *E. quagga* | 2 | 0 | 2 | 0 | 2 | 0 | 0 | 100 | 0 | 100 | 0 |
| **Gladysvale** *E. capensis* | 4 | 0 | 4 | 0 | 4 | 0 | 0 | 100 | 0 | 100 | 0 |
| **Plovers Lake** *E. quagga* | 3 | 0 | 3 | 0 | 3 | 0 | 0 | 100 | 0 | 100 | 0 |
| **Swartkrans** *E. capensis* | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 100 | 0 | 100 | 0 |
| **Makapansgat** *E. capensis* | 5 | 1 | 4 | 0 | 5 | 0 | 20 | 80 | 0 | 100 | 0 |
| **Kalkbank** *E. capensis* | 13 | 2 | 11 | 0 | 12 | 1 | 15.4 | 84.6 | 0 | 92.3 | 7.69 |
| **Kalkbank** *E. quagga* | 20 | 1 | 19 | 0 | 19 | 1 | 5 | 95 | 0 | 95 | 5 |
| **Coopers Cave** *E. capensis* | 2 | 0 | 2 | 0 | 2 | 0 | 0 | 100 | 0 | 100 | 0 |
| **Swallow Hole** *E. capensis/quagga* | 17 | 1 | 16 | 0 | 17 | 0 | 5.9 | 94.1 | 0 | 100 | 0 |
| **Swallow Hole** *E. quagga* | 2 | 0 | 2 | 0 | 2 | 0 | 0 | 100 | 0 | 100 | 0 |
| **Cave of Hearths** *E. capensis* | 3 | 0 | 3 | 0 | 3 | 0 | 0 | 100 | 0 | 100 | 0 |
| **Cave of Hearths** *E. quagga* | 13 | 1 | 12 | 0 | 13 | 0 | 7.7 | 92.3 | 0 | 100 | 0 |
| **Spitskop** *E. capensis* | 8 | 0 | 8 | 0 | 8 | 0 | 0 | 100 | 0 | 100 | 0 |

**Table 3.5** The 26 'typical' extant species and their assigned dietary categories used in the generation of the hierarchal cluster analysis (Fortelius and Solounias 2000). G = grazer, MF = mixed feeder, B = browser.

| Order | Family | Species | Dietary Category |
|---|---|---|---|
| **Artiodactyla** | Bovidae | American plains bison, *Bison bison* | G |
| **Perissodactyla** | Rhinocerotidae | White rhinoceros, *Ceratotherium simum* | G |
| **Perissodactyla** | Equidae | Plains zebra, *Equus quagga* | G |
| **Artiodactyla** | Bovidae | Topi, *Damaliscus lunatus* | G |
| **Artiodactyla** | Bovidae | Wildebeest, *Conochaetes taurinus* | G |
| **Artiodactyla** | Bovidae | Hartebeest, *Alcelaphus buselaphus* | G |
| **Artiodactyla** | Bovidae | Sable antelope, *Hippotragus niger* | G |
| **Artiodactyla** | Bovidae | Roan antelope, *Hippotragus equinus* | G |
| **Artiodactyla** | Bovidae | Bohor reedbuck, *Redunca redunca* | G |
| **Artiodactyla** | Bovidae | Common waterbuck, *Kobus ellipsiprymnus* | G |
| **Artiodactyla** | Bovidae | Impala, *Aepyceros melampus* | MF |
| **Artiodactyla** | Bovidae | Serow, *Carpicornus sumatraensis* | MF |
| **Artiodactyla** | Cervidae | Wapiti, *Cervus canadensis* | MF |
| **Artiodactyla** | Bovidae | Eland, *Taurotragus oryx* | MF |
| **Artiodactyla** | Bovidae | Bushbuck, *Tragelaphus scriptus* | MF |
| **Artiodactyla** | Bovidae | Grant's gazelle, *Gazella granti* | MF |
| **Artiodactyla** | Bovidae | Thomson's gazelle, *Gazella thomsoni* | MF |
| **Artiodactyla** | Bovidae | Muskox, *Ovibos moschatus* | MF |
| **Artiodactyla** | Cervidae | Mule deer, *Odocoileus hemionus* | B |
| **Artiodactyla** | Giraffidae | Giraffe, *Garaffa camelopardalis* | B |
| **Perissodactyla** | Rhinocerotidae | Sumatran rhinoceros, *Dicerorhinus sumatraensis* | B |
| **Artiodactyla** | Giraffidae | Okapi, *Okapi johnstoni* | B |
| **Artiodactyla** | Cervidae | White-tailed deer, *Odocolieus virginianus* | B |
| **Perissodactyla** | Rhinocerotidae | Black rhinoceros, *Diceros bicornis* | B |
| **Artiodactyla** | Cervidae | Moose, *Alces alces* | B |
| **Perissodactyla** | Rhinocerotidae | Javan rhinoceros, *Rhinoceros sondaicas* | B |

# Chapter Four

## Results

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### 4.1 Geometric Morphometric Analyses

4.1.1 Relative Warp Analyses

Relative warp analyses were carried out to investigate whether *E. capensis* had a unique occlusal enamel shape in comparison to that of a variety of extinct and extant equids. Fig. 4.1.1 presents a plot of RW1 against RW2 scores (accounting for 49.25% of total shape variation within the sample), generated from a relative warp analysis of mandibular teeth. From this figure, it is clear

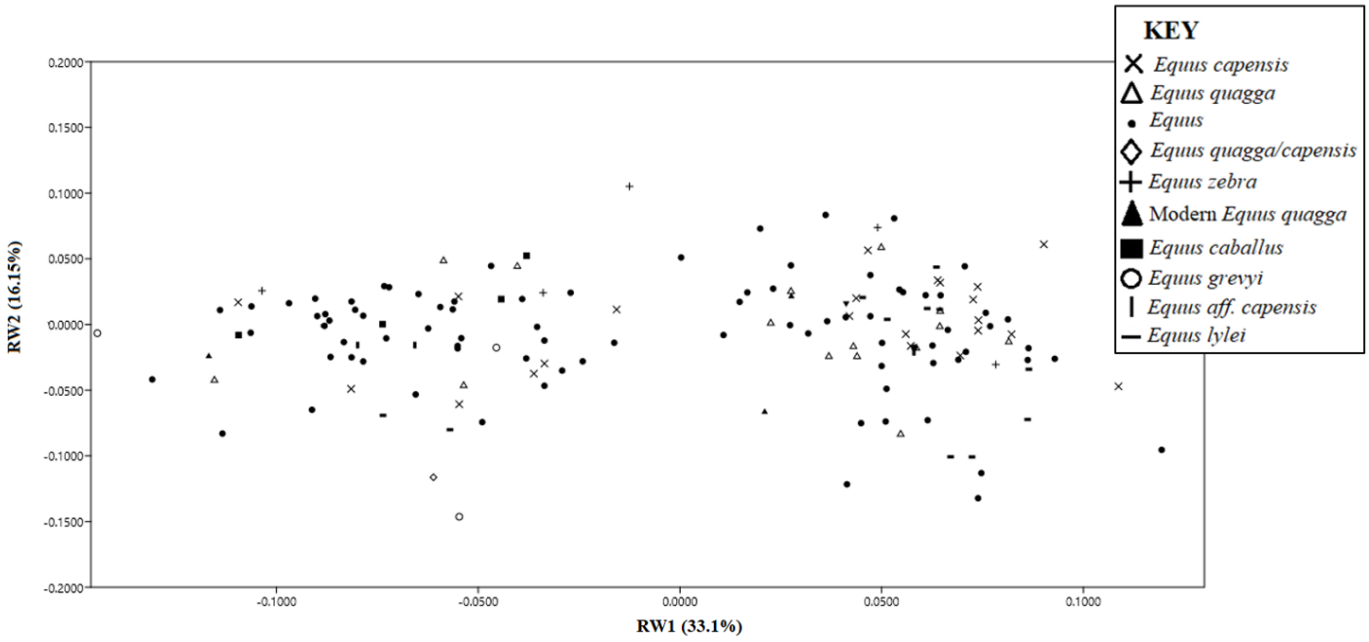


**Figure 4.1.1** Plot of RW1 and RW2 of a relative warp analysis of the mandibular cheek teeth of all equid species included in this study. Specimens labelled '*Equus*' have only been identified to genera in the fossil record.

that *E. capensis* does not separate out from the other species along either axes of variation. *Equus capensis* also shows a wide range of both positive and negative values across RW1 and RW2. A MANOVA was performed on the first five relative warp scores (accounting for 65.61% of the total variation). For this analysis, *E. asinus* and the combined *Equus capensis/quagga* specimens were removed as each is represented by one sample only. Results indicate the presence of significant differences within the total analysed sample (Wilk's Lambda: F=2.233, df=35, $P<0.05$; Pillai trace: F=2.156, df=35, $P<0.05$). Nevertheless, pairwise comparisons were unable to find any significant differences (at $P>0.05$) between the occlusal enamel shape of *E. capensis* and that of all other species, suggesting that (1) it is not the source of this variance, and that (2) its occlusal enamel shape is not unique.

Fig. 4.1.2 presents a plot of RW1 against RW2 scores (accounting for 37.41% of total shape variation within the sample), generated from a relative warp analysis of maxillary teeth. Again, there is no clear separation of *E. capensis* from any of the other species, and the samples illustrate a broad range of variation of occlusal enamel shape, showing positive and negative values along both RW1 and RW2. A MANOVA performed on the first five relative warp scores (58.53% of the total variation) again show a significant difference in the analysed sample (Wilk's Lambda: F=2.584, df=30, $P<0.05$; Pillai trace: F=2.509, df=30, $P<0.05$. *Equus grevyi* and *Equus oldowayensis* were removed from this statistical analysis, as they are represented by one sample each. Pairwise comparisons show that the only significant differences between groups are between *E. capensis* and *Equus* ($P=0.001$), and *Equus zebra* and *Equus* ($P<0.001$). This result may be influenced by the fact that the *Equus* group includes the highest number of specimens ($N=150$), all of which are of unknown species and therefore could include an entire range of equid species.

Moreover, the larger sample size of maxillary specimens inevitably leads to greater variability, thus emphasis should not be placed on these shape differences. Again, results do not support the assertion that *E. capensis* possessed a unique occlusal enamel shape.

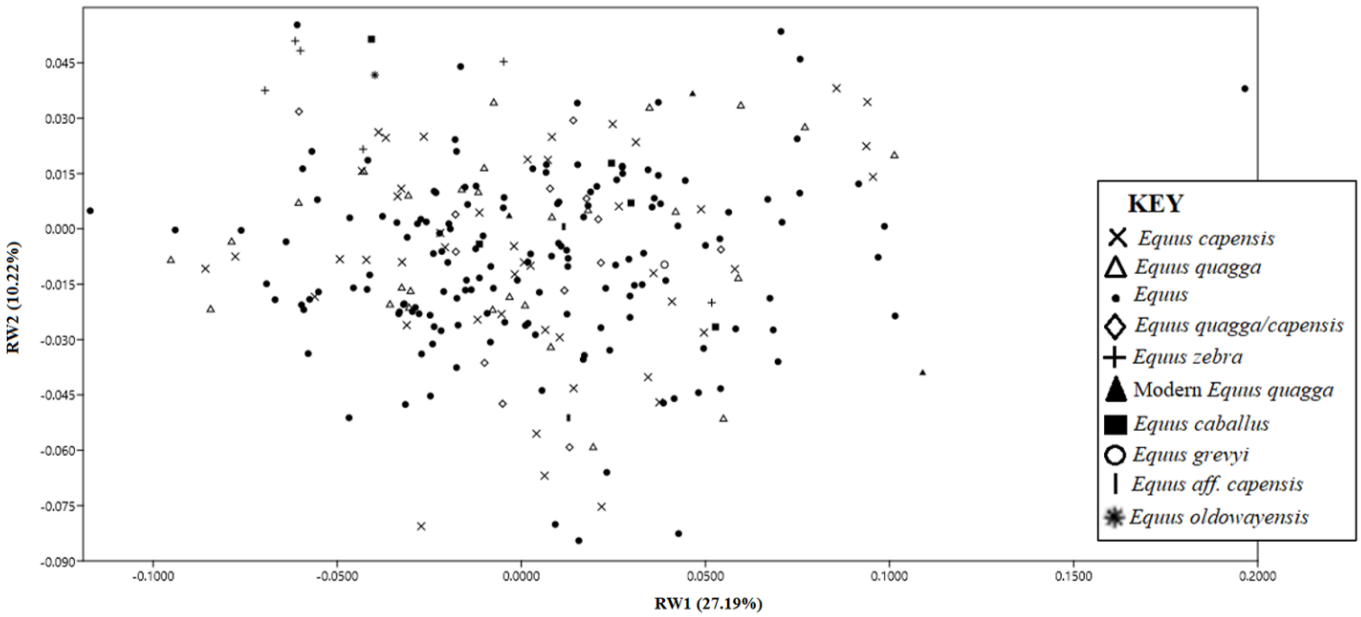


**Figure 4.1.2** Plot of RW1 and RW2 of a relative warp analysis of the maxillary cheek teeth of all equid species included in this study. Specimens labelled '*Equus*' have only been identified to genera in the fossil record.

Ancient DNA evidence suggests a close relationship between *E. capensis* and *E. quagga*. To investigate this relationship from an occlusal enamel shape perspective, I performed relative warp analyses on only *E. capensis*, *E. quagga* and *E. capensis*/*E. quagga* for mandibular and maxillary cheek teeth (Figs. 4.1.3 and 4.1.4). Figure 4.1.3 presents a plot of RW1 against RW2 scores (accounting for 43.27% of total shape variation within the sample), generated from a relative warp analysis of mandibular cheek teeth. The majority of mandibular specimens for both species exhibit similarly positive values along RW1 (68% of *E. capensis* samples and 67% of *E. quagga* samples), and there is no separation from each other in terms of shape variability between the species.

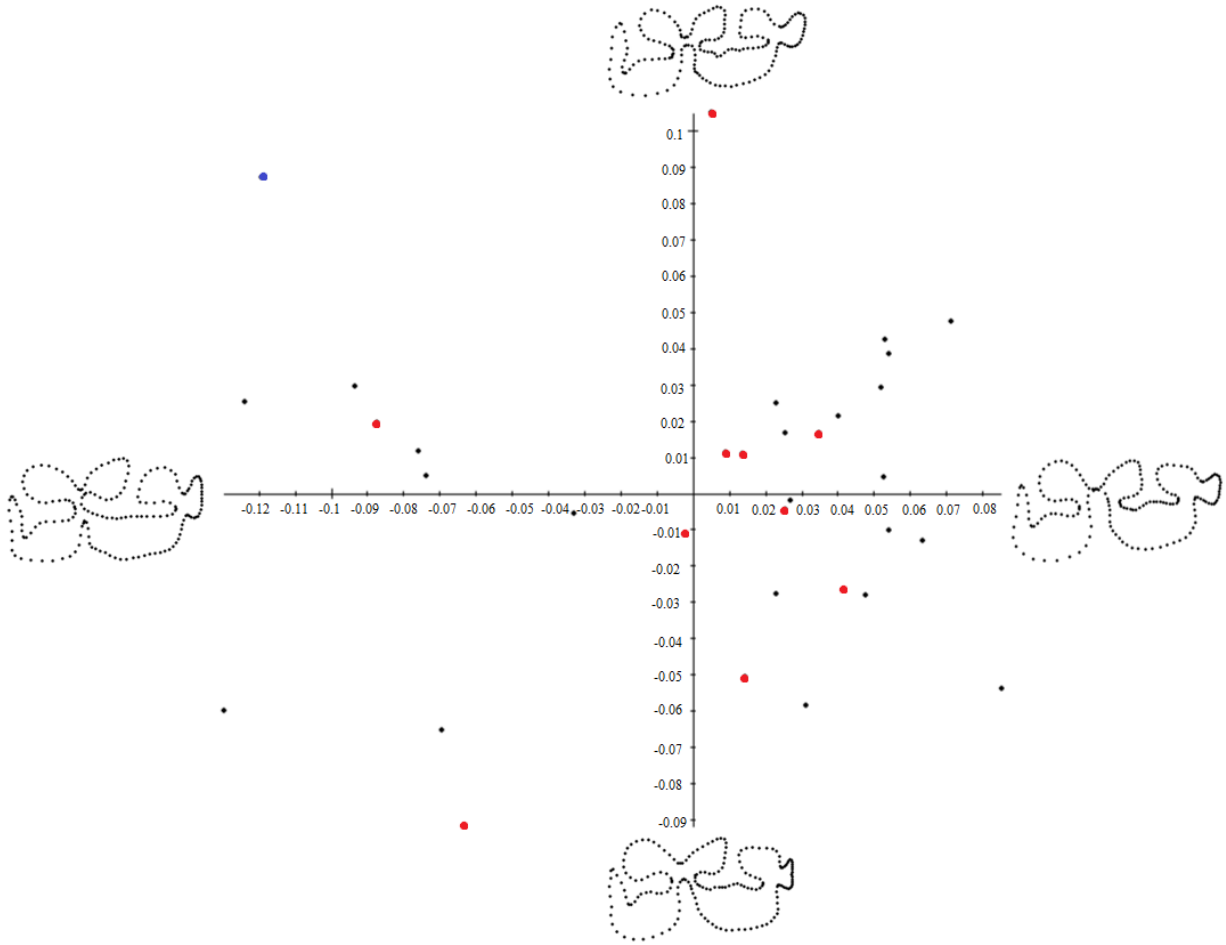


**Figure 4.1.3** Morphospace for all mandibular cheek teeth of specimens identified as *Equus capensis* (black), *Equus quagga* (red), and *Equus capensis/quagga* (blue). The shape changes of the enamel folding along the major axes of variations (PC1 x-axis = 30.14% variance, and PC2 y-axis = 13.03% variance) are displayed for the extreme values of each axis.

Furthermore, the maxillary sample shows an even broader flexibility of shape (Fig. 4.1.4), with specimens of both species (as well as those marked as '*Equus capensis/quagga*') showing positive and negative values along both RW1 and RW2. This slightly increased variation within the maxillary sample is likely due to the overall larger sample size. To test whether there are any statistically significant shape differences between the samples, a MANOVA was performed on the first five relative warp scores for both the mandibular (accounting for 68% of the total variation)

and maxillary teeth (accounting for 64.01% of the total variation). For both mandibular (Wilk's Lambda: F=0.189, df=5, *P*=0.964; Pillai trace: F=0.189, df=5, *P*=0.964), and maxillary specimens (Wilk's Lambda: F=1.479, df=10, *P*=0.152; Pillai trace: F=1.495, df=10, *P*=0.146), it is clear that there is no significant difference in occlusal enamel shape between *E. capensis*, *E. quagga* and *E. capensis*/*E. quagga*.

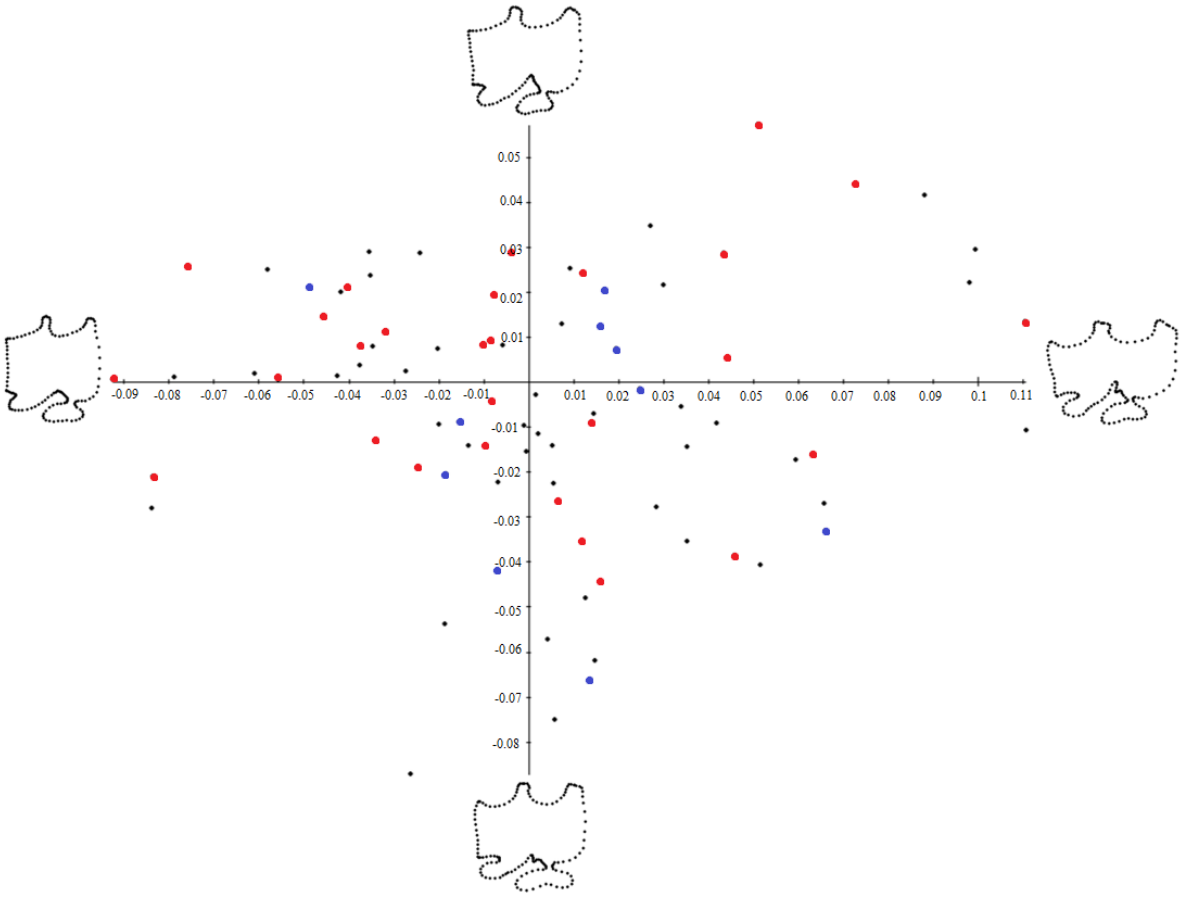


**Figure 4.1.4** Morphospace for all maxillary cheek teeth of specimens identified as *Equus capensis* (black), *Equus quagga* (red), and *Equus capensis/quagga* (blue). The shape changes of the enamel folding along the major axes of variations (PC1 x-axis = 28.48% variance, and PC2 y-axis = 11.84% variance) are displayed for the extreme values of each axis.

The results of relative warp analyses for maxillary and mandibular cheek teeth for only specimens that have been classified as *E. capensis* are presented (Figs. 4.1.5 and 4.1.6). The analysis was

performed in order to evaluate the specific enamel features that have been used by previous researchers to identify *E. capensis* teeth. Despite the majority (68%) of the mandibular specimens showing positive values along RW1 (Fig. 4.1.5), there is still variation within the sample, as specimens show extremely positive and negative values along both RW2 and RW1. The cumulative

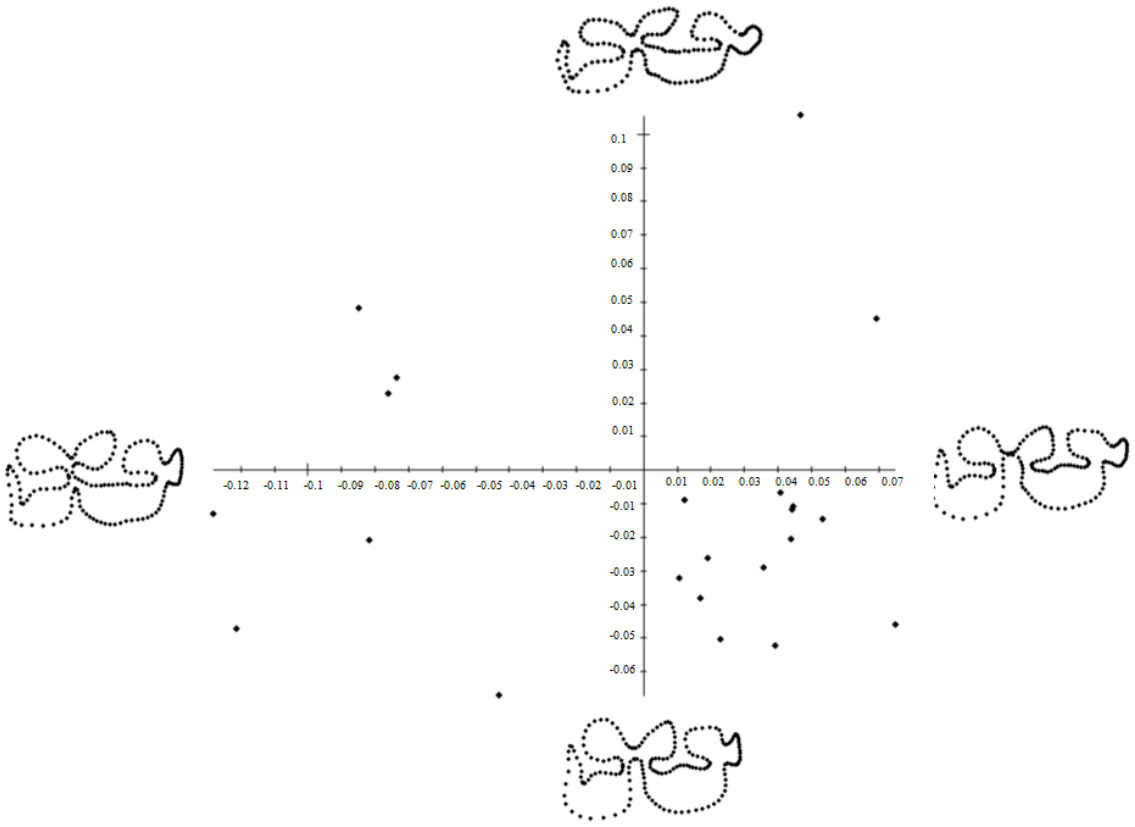


**Figure 4.1.5** Morphospace for all mandibular cheek teeth of specimens identified as *Equus capensis*. The shape changes of the enamel folding along the major axes of variations (PC1 x-axis = 33.55% variance, and PC2 y-axis = 12.63% variance) are displayed for the extreme values of each axis. Majority do fall in one area but great outliers, still plenty of room for variation.

variation of RW1 and RW2 is 46.18%. The protoconid varies from short and broad along negative PC2, to long and narrow along positive PC2. The hypoconid also shows evident variation, from wide and rounded along negative PC2, to longer and narrower along positive PC2. The ectoflexid

is also extremely variable, with some specimens low and pointed (negative PC1), and others round and high up – some nearly meeting the linguaflexid (positive PC1). The metaconid and metastylid also diverge; although no specimens show these features to be triangular, they do vary from either oval shaped or circular shaped. Lastly, the hypoconulid also differs widely across specimens, some being thin and slightly pointed along negative PC1 and P2C, while others are wider and more rounded along positive PC1 and PC2.

In the case of the *E. capensis* maxillary relative warps analysis, there is arguably even more variation (Fig. 4.1.6), with all specimens spread broadly across the extremes of both RW1 and

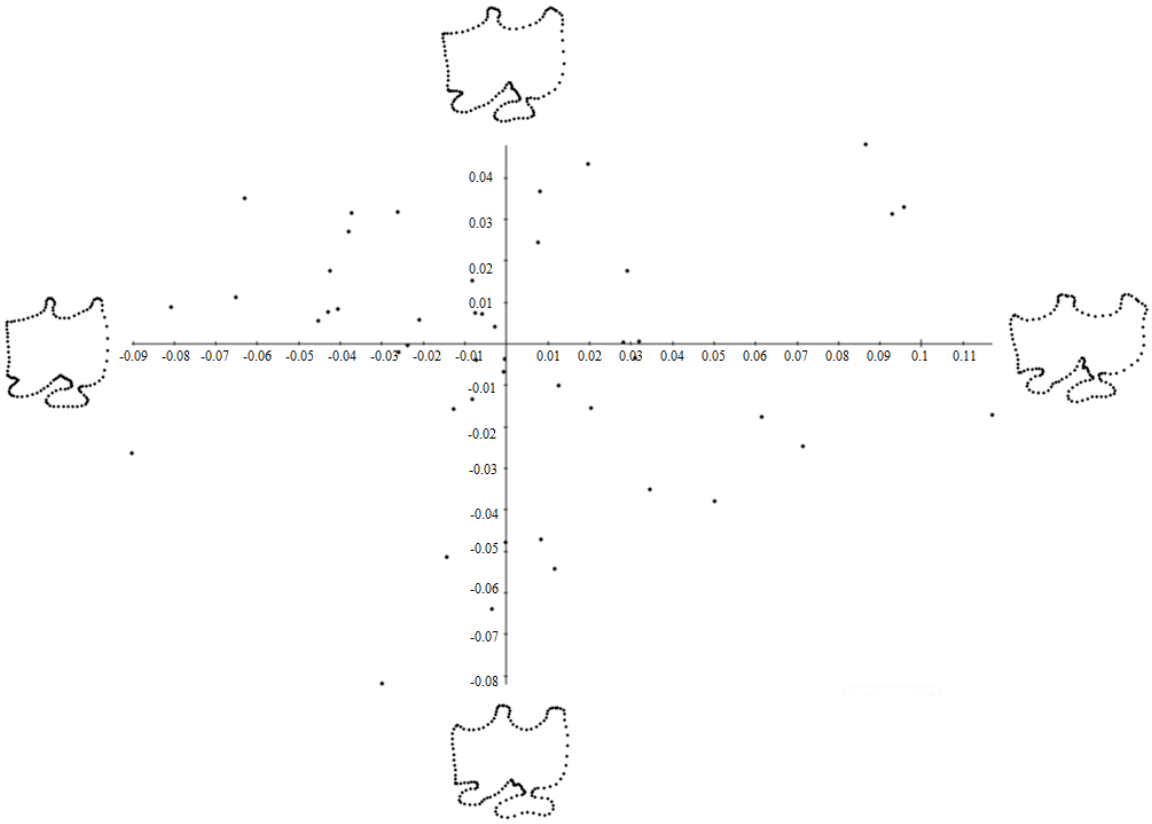


**Figure 4.1.6** Morphospace for all maxillary cheek teeth of specimens identified as *Equus capensis*. The shape changes of the enamel folding along the major axes of variations (PC1 x-axis = 30.61% variance, and PC2 y-axis = 13.05% variance) are displayed for the extreme values of each axis.

RW2 (which account for 43.66% of the total variation). Again, this is perhaps due to the larger sample size of maxillary *E. capensis* cheek teeth, with increased sample size resulting in increased variability. A larger sample size of mandibular teeth could confirm this, and would perhaps show similarly widely distributed variation. Parastyles in *E. capensis* cheek teeth are in some specimens pronounced and in others not at all, and the same can be said for the presence of a pli caballine fold. Mesostyles also vary, from small and thin to broad and fairly large. The hypoconal groove can be deep or shallow, and by extension the hypocone varies in its size. Lastly, the protocone also varies in size, in some cases protruding more than in others. The wide range of variation in occlusal patterns of both mandibular and maxillary teeth does not agree with the strict patterns assigned by previous researchers to *E. capensis*, which have been presented as considerably narrower.

### 4.1.2 Centroid Size

Centroid size for maxillary and mandibular cheek teeth of all *Equus* species are presented (Figs. 4.1.7 and 4.1.8). One-way analysis of variances (ANOVAs) were used for inter-group comparison to test whether size discriminates between the populations. All Levene's tests results are from the medians, and all Mann–Whitney pairwise test results are raw *P* values with sequential Bonferroni significance. Although *Equus* and *E. capensis* overlap in the mandibular tooth size (Fig. 4.1.7), it is primarily the highest values of the interquartile range of *Equus* that overlap with the central 50% of the *E. capensis* specimens. The *Equus* sample is extremely large and consists of various unknown species, so this is likely the reason for its large interquartile range. Despite the overlap there is still a significant difference in median size between the two (Mann–Whitney: $P<0.05$, Kolmogorov Smirnov: $P<0.05$, Levene's test, $P=0.278$). There is considerable overlap between *E.*

*capensis* and *Equus aff. capensis*, which resemble each other in size (Mann–Whitney: *P*=0.834, Kolmogorov Smirnov: *P*=0.924, Levene's test, *P*=0.901). While there is also overlap between *E.*

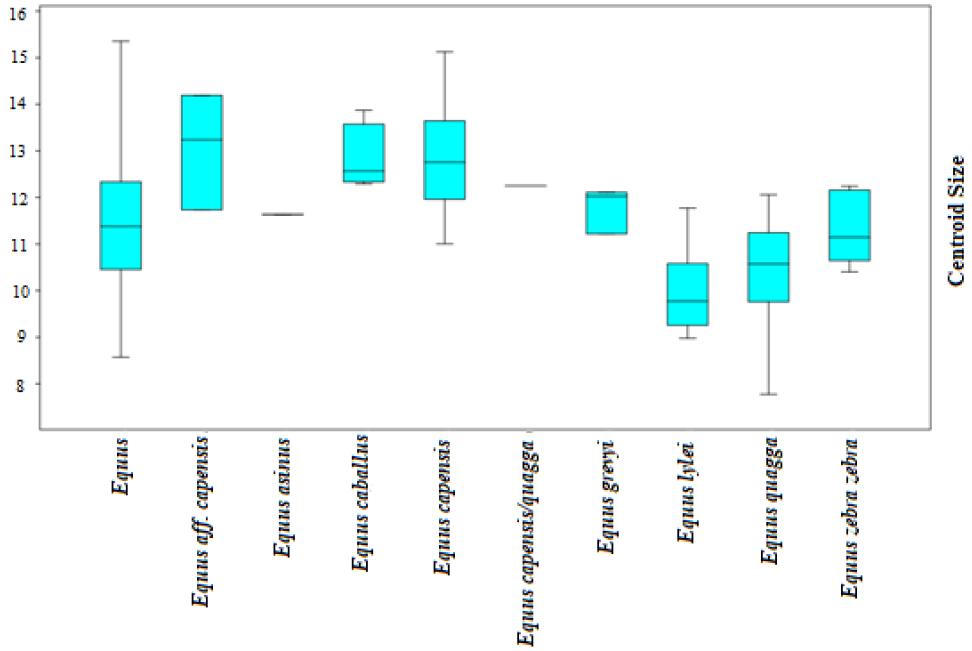


**Figure 4.1.7** Box plots summarizing inter-specific variation in *Equus* mandibular dentition centroid size. The vertical line within the blue box marks the median of the sample. The length of each box signifies the range within which the central 50% of the values fall, with the box edges at the first and third quartiles. The highest and lowest values of the interquartile range are represented by the whiskers.

*caballus* and *E. capensis*, this is likely more a result of the small sample size of *E. caballus* (*N*=4). Moreover, many modern domestic horses are bred for their size, and consequently this sample likely includes larger sized horses. The *E. capensis* median centroid size is 12.756, higher than all other species groups in the mandibular sample. Median centroid size of *E. capensis* is also significantly different to that of *E. quagga*, which also shows very low values in the lower interquartile range (Mann–Whitney: *P*<0.05, Kolmogorov Smirnov: *P*<0.05, Levene's test, *P*=0.922).

In the case of the maxillary sample (Fig. 4.1.8), the wide range of high interquartile values of *Equus* is again likely due to the large sample size (*N*=148) coupled with expected high levels of between-species variation within the sample. Although there is overlap between *Equus* and *E.*

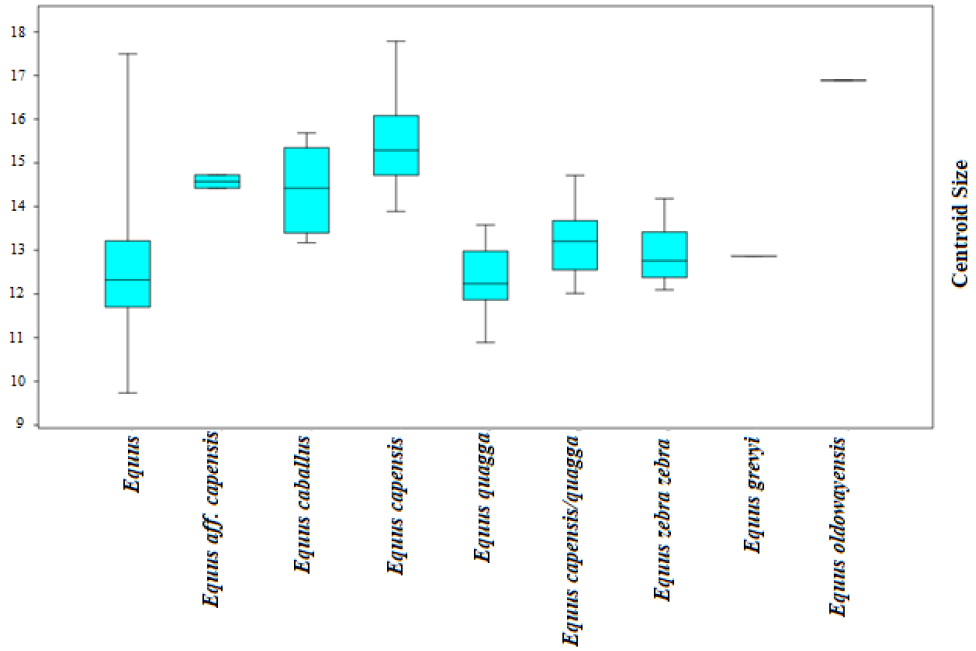


**Figure 4.1.8** Box plots summarizing inter-specific variation in *Equus* maxillary dentition centroid size. The vertical line within the blue box marks the median of the sample. The length of each box signifies the range within which the central 50% of the values fall, with the box edges at the first and third quartiles. The highest and lowest values of the interquartile range are represented by the whiskers.

*capensis* as a result of this, the values of the central 50% are entirely separated between the two groups, with *E. capensis* showing a much larger range of values (Mann–Whitney: $P<0.05$, Kolmogorov Smirnov: $P<0.05$, Levene's test, $P=0.045$). Interestingly, the highest interquartile values of *E. quagga* do not overlap with the lowest interquartile values of *E. capensis* (Fig. 4.1.9), separating the two out entirely from one another in their centroid sizes (Mann–Whitney: $P<0.05$, Kolmogorov Smirnov: $P<0.05$, Levene's test, $P=0.062$). The same pattern of separation is seen in the mandibular sample (Fig. 4.1.10). *Equus capensis/quagga* is slightly closer in size to *E. quagga*

than it is to *E. capensis*, but appears to be largely intermediate between the two in overall centroid size (Fig. 4.1.11). The median centroid size of *E. capensis/quagga* is also nearly equidistant between *E. capensis* and *E. quagga* (*E. capensis/quagga*=13.205, *E. quagga*=12.237, *E. capensis*=15.289). It appears as though specimens classified as *E. capensis/quagga* may have been labelled as such on the basis of their intermediate size.

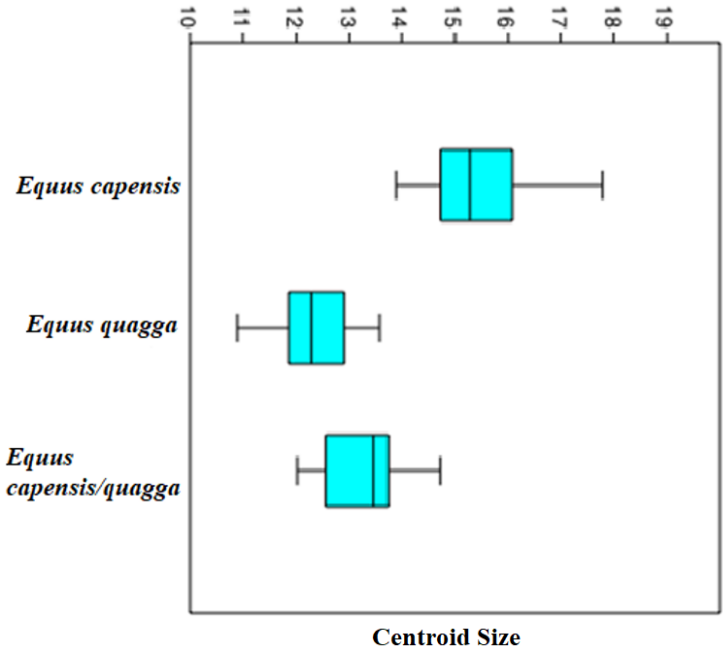


**Figure 4.1.9** Box plots comparing maxillary dentition centroid size in *Equus capensis* and fossil *Equus quagga*. The vertical line within the blue box marks the median of the sample. The length of each box signifies the range within which the central 50% of the values fall, with the box edges at the first and third quartiles. The highest and lowest values of the interquartile range are represented by the whiskers.

Overall, in both the mandibular and maxillary samples, *E. capensis* is clearly distinguished from the other equid species in terms of its size (Fig. 4.1.11), but illustrates a general similarity with *E. quagga* in occlusal enamel shape and shape variation. The range of shape variation for both *E. capensis* and *E. quagga* is wide, particularly in the better represented maxillary sample. Added to

this, both groups show a similar type of shape variation for both mandibular and maxillary cheek teeth. This is more evident in the smaller mandibular sample. Not only does *E. capensis* show clear differentiation from *E. quagga* in size, but it separates in size from all other equid species as well. This is the case for both the upper and lower teeth. The morphospace for *E. capensis* encompasses considerable variation for both types of cheek teeth, with values along extreme ends of both RW1 and RW2 illustrating an intraspecific variation wider than previously recognized.

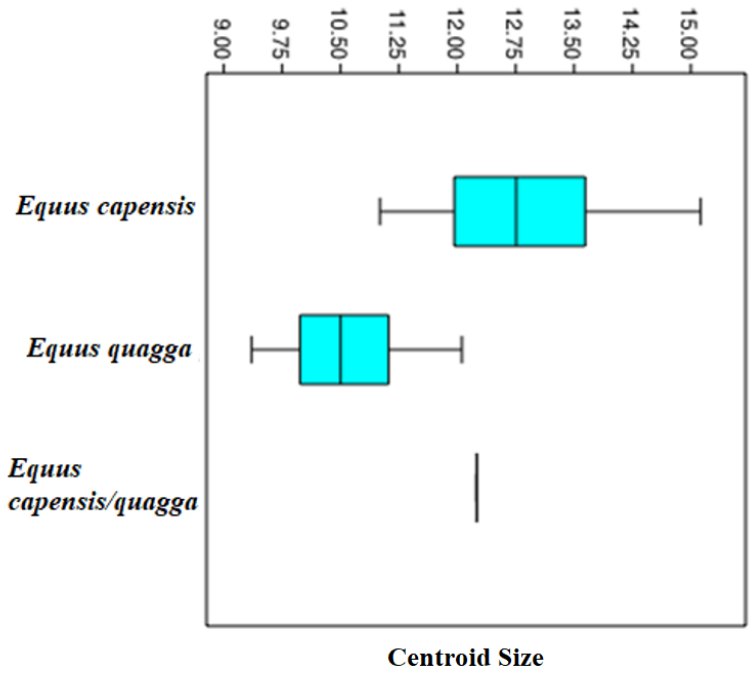


**Figure 4.1.10** Box plots comparing mandibular dentition centroid size in *Equus capensis* and fossil *Equus quagga*. The vertical line within the blue box marks the median of the sample. The length of each box signifies the range within which the central 50% of the values fall, with the box edges at the first and third quartiles. The highest and lowest values of the interquartile range are represented by the whiskers.

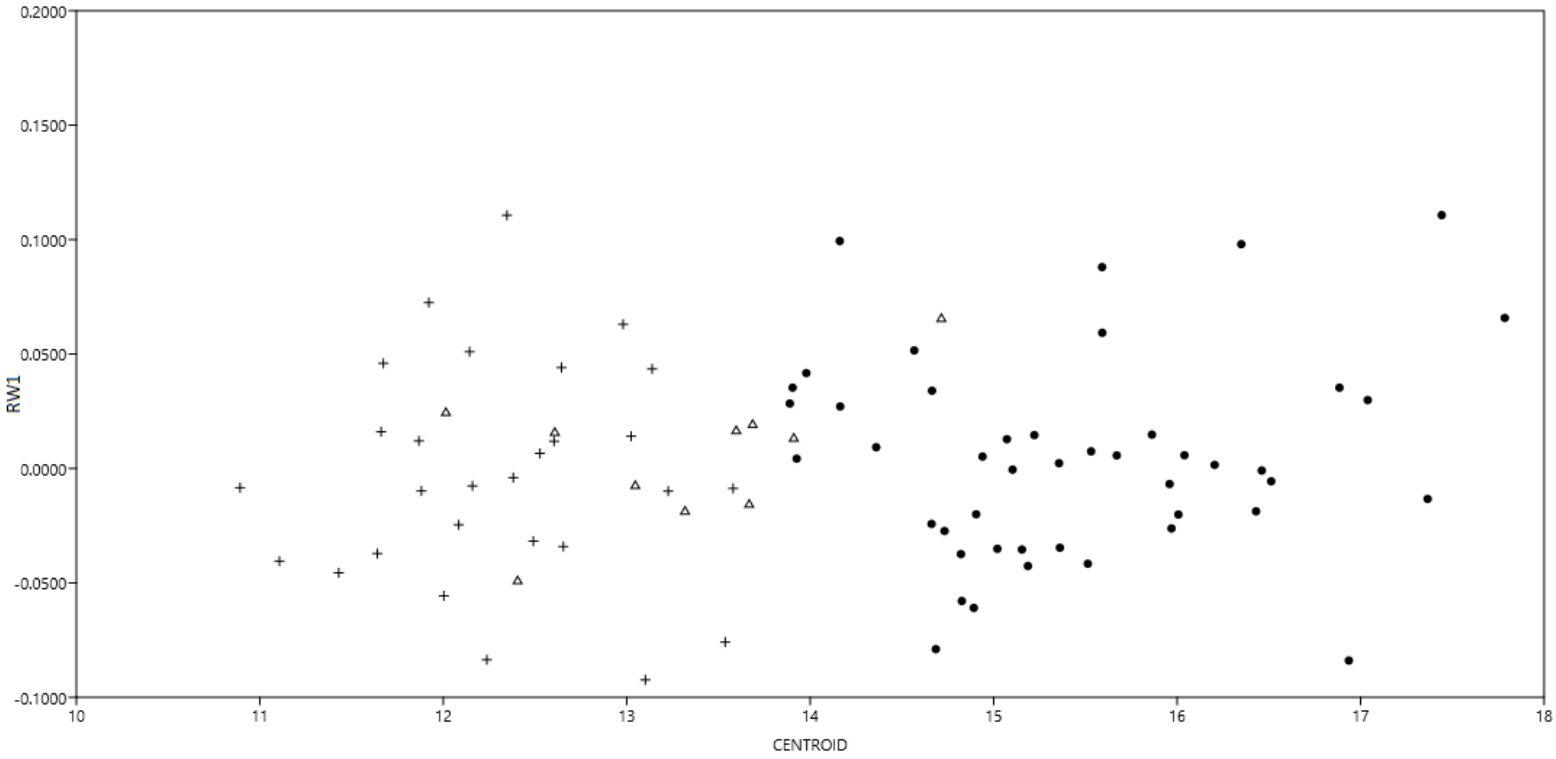


**Figure 4.1.11** Variation in maxilla centroid size of *Equus capensis* (dots), *Equus quagga* (plus signs), and *Equus quagga/capensis* (triangles). All specimens delineated as *Equus capensis/quagga* fall within the centre of the average centroid size between the other two species groups.

## 4.2 Linear Measurements

Dental occlusal surface length and breadth measurements for a range of equids were subjected to principal components analyses and the first two PC scores plotted against each other (Figs. 4.2.1 and 4.2.2). In both the mandibular and maxillary samples, *E. capensis* is clearly separated from the other equids along PC1, but not PC2. Positions along PC1 are primarily driven by size, thus it is not much of a surprise given the generally larger size of teeth in the *E. capensis* category. One–tailed t-tests were performed on PC1s and PC2s to test for significant differences between *E. capensis* and the rest of the *Equus* sample. Again, in both the mandibular (*t*-value is 10.81;

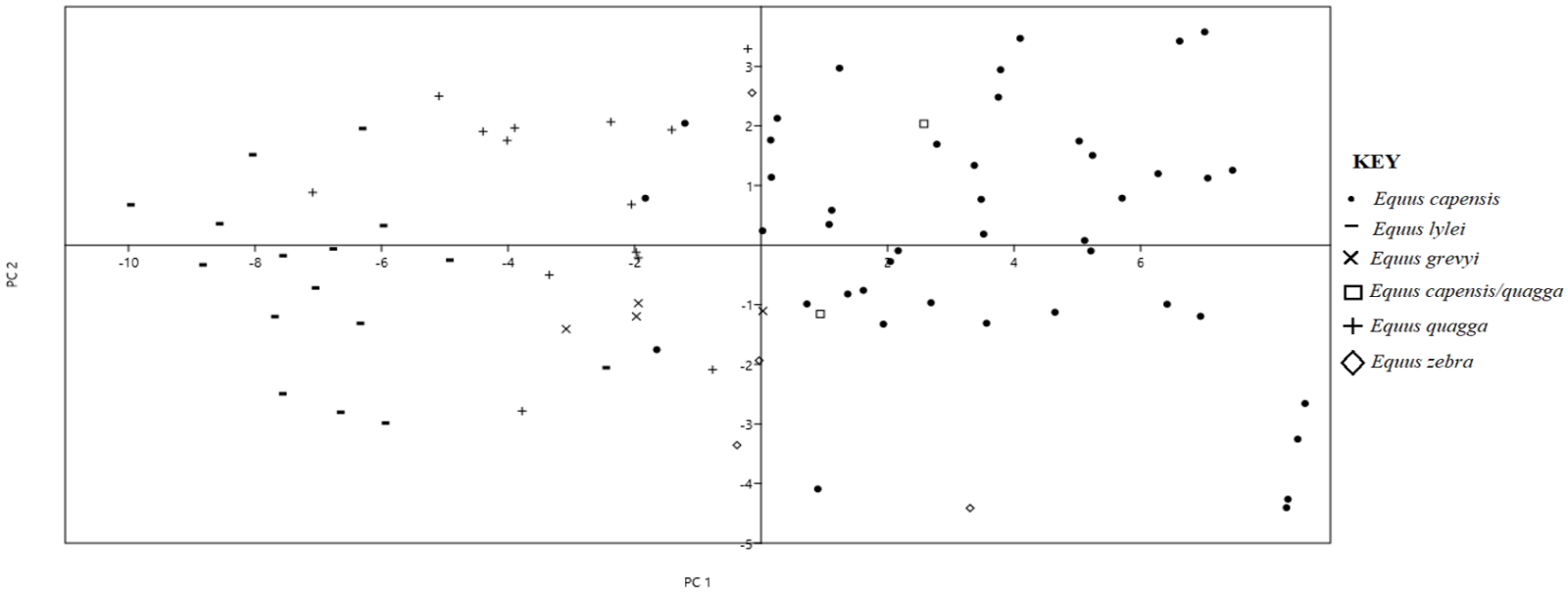


**Figure 4.2.1** Principal components analysis of equid mandibular cheek teeth length and breadth. X-Axis: PC1 (85.96% variance) and Y-Axis: PC2 (14.04% variance).

*P*<0.001) and maxillary (*t*-value is 13.198; *P*<0.001) samples, *E. capensis* differs significantly from the rest in terms of PC1 scores. This is however not the case with PC2 where both the mandibular (*t*-value is 1.034; *P*=0.152) and maxillary (*t*-value is 0.593; *P*=0.278) teeth are not significantly different between *E. capensis* and the other samples.

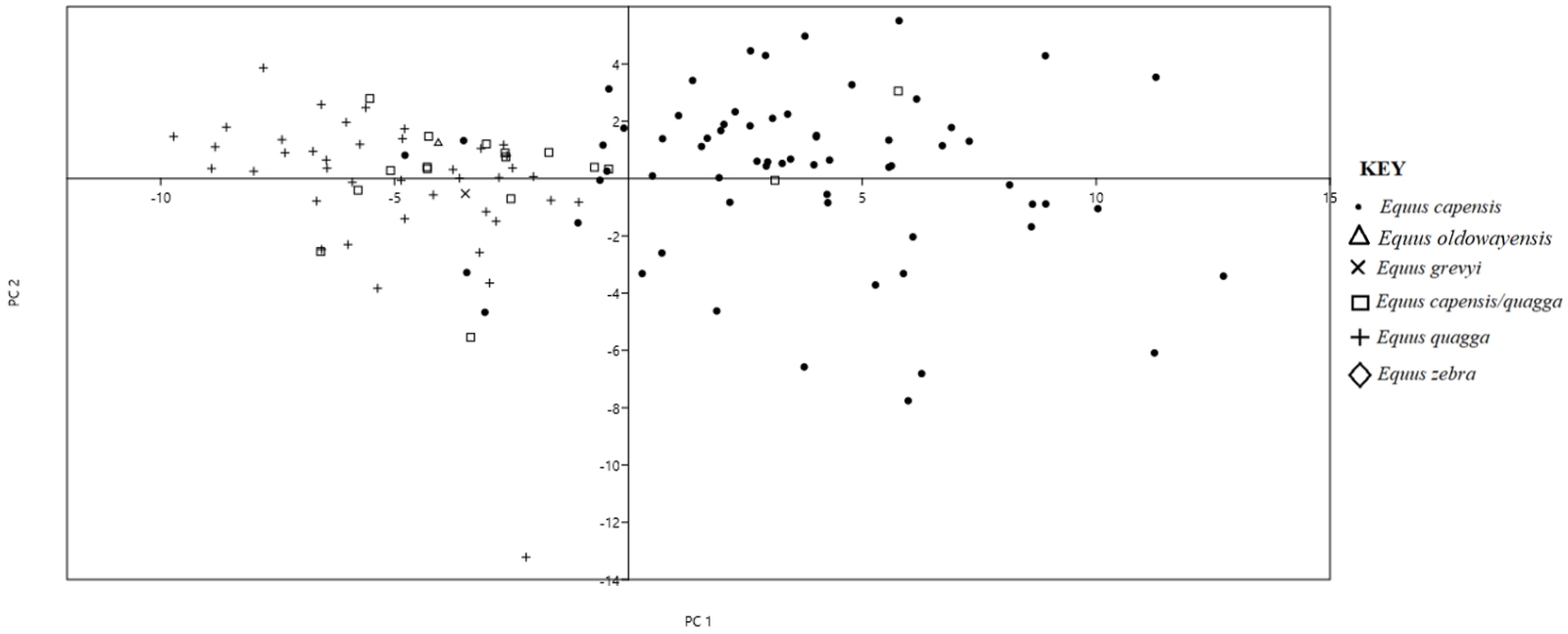


**Figure 4.2.2** Principal components analysis of equid maxillary cheek teeth length and breadth. X-Axis: PC1 (81.02% variance) and Y-Axis: PC2 (18.98% variance).

### 4.3 Occlusal Enamel Index

The results of OEI analysis for maxillary cheek teeth in *E. capensis* and five other equid groups are presented (Fig. 4.3.1). The samples fell in a range of 7 – 18, with both *E. capensis* and *E. quagga* in a range of 8 – 11. *Equus asinus* has the lowest OEI (mean=7.856) and *Equus caballus* has the highest (mean=15.376). The two groups that are the most similar in overall complexity are *E. capensis* and *E. quagga* – difference between OEI means=0.552 – with *E. capensis* showing slightly higher complexity levels (Mann–Whitney: $P<0.001$, Kolmogorov Smirnov: $P=0.002$, Levene's test, $P=0.443$). Despite a significant difference in the two-sample tests, the difference between *E. capensis* and *E. quagga* is much smaller than that between any two other species in the analysis (Table 4.1). The median of *E. capensis* (9.625) is closer to that of *E. quagga* (9.143) than it is to any other equid, including the notably large *E. grevyi.* When other groups are tested against

each other, even higher levels of significant differences emerge – *E. quagga* vs. modern *E. quagga*: Mann–Whitney: $P$=0.004, Kolmogorov Smirnov: $P$=0.011, Levene's test, $P$=0.346; *E. capensis* vs. *E. grevyi*: Mann–Whitney: $P$<0.001, Kolmogorov Smirnov: $P$<0.001, Levene's test, $P$=0.044; *E. capensis* vs. *E. caballus*: Mann–Whitney: $P$<0.001, Kolmogorov Smirnov: $P$<0.001, Levene's test, $P$<0.001.

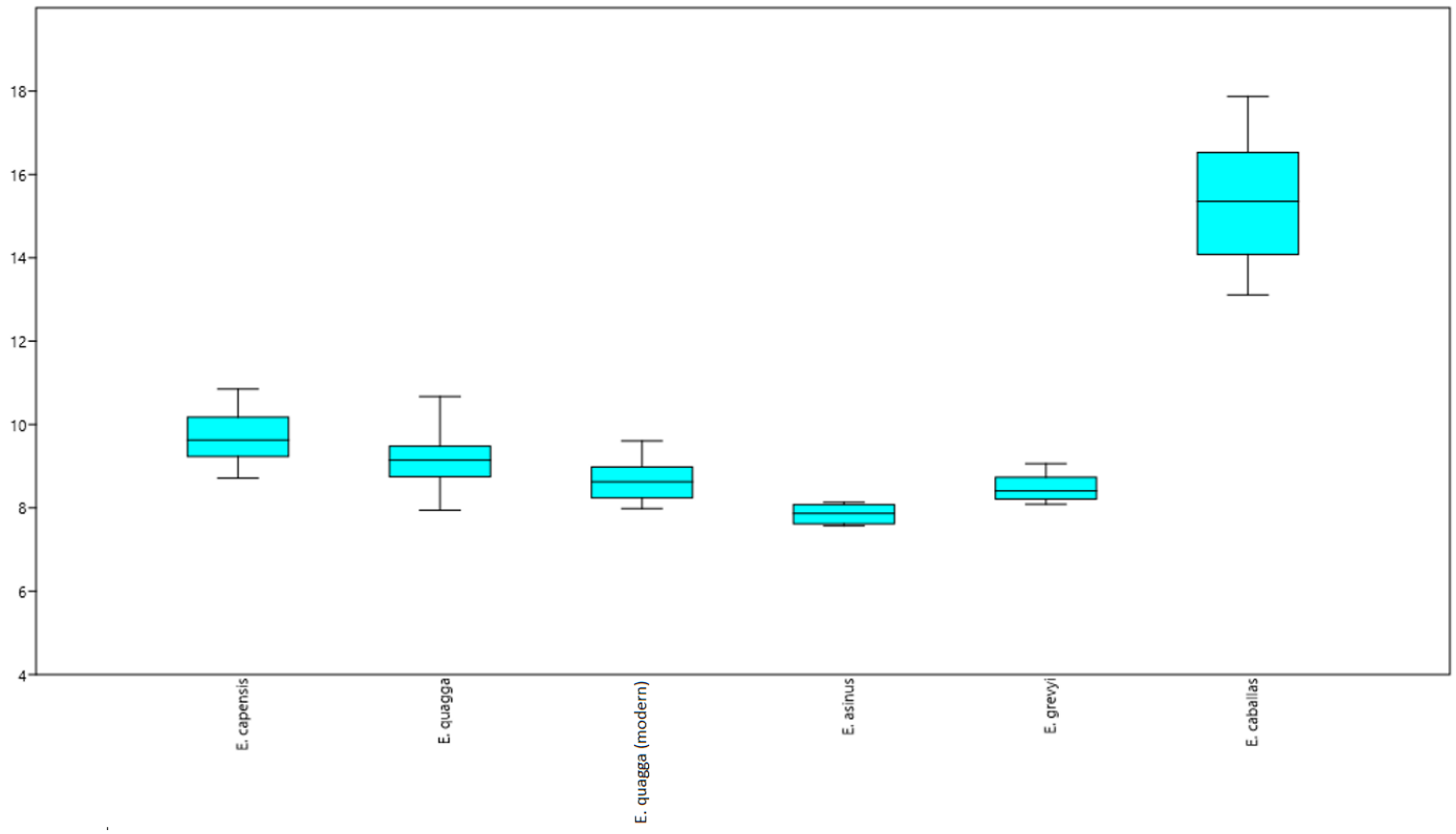


**Figure 4.3.1** Box plots illustrating OEI variation in six equid groups (raw OEI data of modern *E. quagga*, *E. asinus*, *E. grevyi* and *E. caballus* from Famoso and Davis 2014). The vertical line in the center of the box marks the median of the sample. The blue of each box represents the range within which the central 50% of the values fall, with the box edges at the first and third quartiles. The whiskers extend to the highest and lowest values of the interquartile range.

**Table 4.1** Summary statistics of Occlusal Enamel Complexity

| | *E. capensis* | *E. quagga* | *E. quagga (modern)* | *E. asinus* | *E. grevyi* | *E. caballus* |
|---|---|---|---|---|---|---|
| **Number** | 39 | 29 | 24 | 6 | 6 | 24 |
| **Minimum** | 8.710957 | 7.941864 | 7.98212 | 7.568455 | 8.089484 | 13.11263 |
| **Maximum** | 10.85172 | 10.66919 | 9.603751 | 8.132244 | 9.058945 | 17.8738 |
| **Mean** | 9.689434 | 9.137485 | 8.675346 | 7.855619 | 8.472338 | 15.3758 |
| **Variance** | 0.3798563 | 0.35364 | 0.1995502 | 0.05057241 | 0.1142423 | 2.328735 |
| **Standard deviation** | 0.6163248 | 0.5946764 | 0.4467104 | 0.2248831 | 0.3379975 | 1.526019 |
| **Median** | 9.624999 | 9.142944 | 8.62375 | 7.866223 | 8.405763 | 15.35231 |
| **25th percentile** | 9.233623 | 8.74443 | 8.238155 | 7.619193 | 8.210718 | 14.08174 |
| **75th percentile** | 10.17589 | 9.479088 | 8.981732 | 8.081407 | 8.731946 | 16.52793 |

## 4.4 Mesowear

Fig. 4.4.1 presents the result of a hierarchical cluster analysis calculated using four variables (%h, %s, %r, %b). The 26 comparative extant species, and the *E. capensis* and *E. quagga* samples from various sites, are classified into three broad dietary classes: grazers, browsers and mixed feeders. To the left of the cluster are the browsers (brown), in the centre are the mixed feeders (green) and to the right are the grazers (yellow). All *E. capensis* and *E. quagga* samples fall within the cluster of extant obligate grazers, regardless of the site from which they are derived. In contrast to the mesowear analysis of Kaiser and Franz-Odendaal (2004), which was conducted at a single site, the current study found *E. capensis* to be a grazer rather than a mixed feeder. This result is in accordance with the mesowear analysis of Stynder (2009), that also classes *E. capensis* as an obligate grazer. The sample size for *E. capensis* in the current study ($n$=66) are, as with Stynder's (2009) analysis, much larger than the sample size of Kaiser and Franz-Odendaal's (2004) analysis ($n$=14). It is interesting that with the exception of *E. capensis* from Kalkbank and *E. capensis* from Makapansgat, all the fossil equid samples cluster next to each other. The normalized distance at the branching point between all groups is so close that it is not even visible on the hierarchical cluster, indicating incredibly similar mesowear signatures. Such similar mesowear patterns suggest

a very similar diet. Added to this, all groups display a significant majority of high rather than low cusps, and round rather than blunt or sharp cusp shapes (Fig. 4.4.2). The lack of variation between percentages of high and low cusps as well as between percentages of sharp, round and blunt cusps (Table 3.4) further indicates not only the similarity in diet between *E. capensis* and *E. quagga*, but

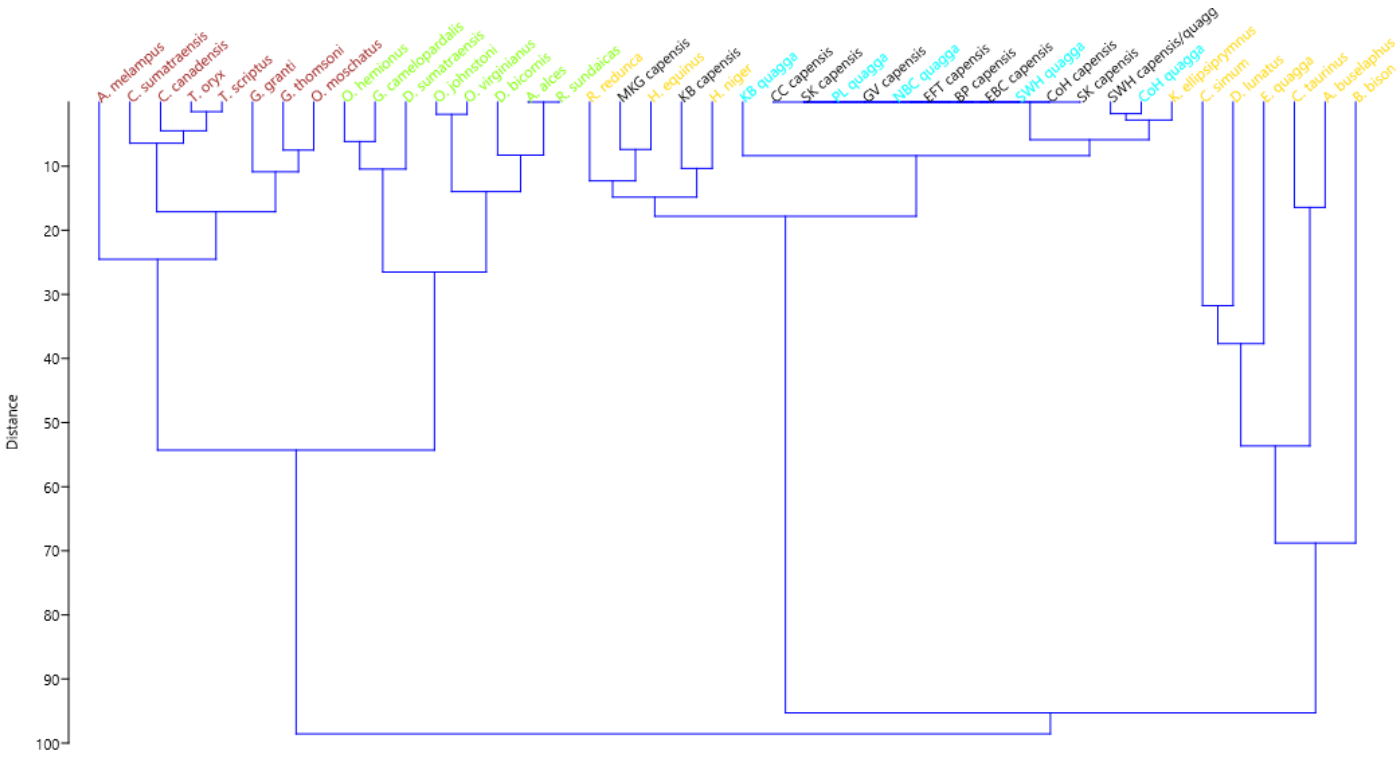


**Figure 4.4.1** Hierarchical cluster diagram of *E. capensis* and *E. quagga* specimens from a variety of localities, compared to a set of 26 'typical' extant species from Fortelius and Solounias (2000). Mesowear variables used are % high, % sharp, % round and % blunt. The brown (leftmost) cluster contains the browsing species, the green contains mixed feeders and the yellow specimens are those of grazers. The black and blue represent *E. capensis* and *E. quagga*, respectively, from different sites. The closer species are in their mesowear signature, the smaller the normalized distance at the branching point. MKG = Makapansgat, KB = Kalkbank, CC = Coopers Cave, SK = Spitskop, PL = Plovers Lake, GV = Gladysvale, NBC = Nelson Bay Cave, EFT = Elandsfontein, BP = Boomplaas, EBC = Elands Bay Cave, SWH = Swallow Hole, CoH = Cave of Hearths.

the full extent to which they are both obligate grazers. Interestingly, the two groups closest to the mixed feeding cluster, and the only two groups that slightly separate out from the rest, are *E. capensis* groups (Kalkbank and Makapansgat), rather than the smaller and supposedly more adaptable *E. quagga*. These results indicate that, despite the fluctuation in environments during the Pleistocene in Africa, and despite their difference in body size, both of these groups utilized grasses rather than browse across the variety of sites analysed. However, mesowear analysis does

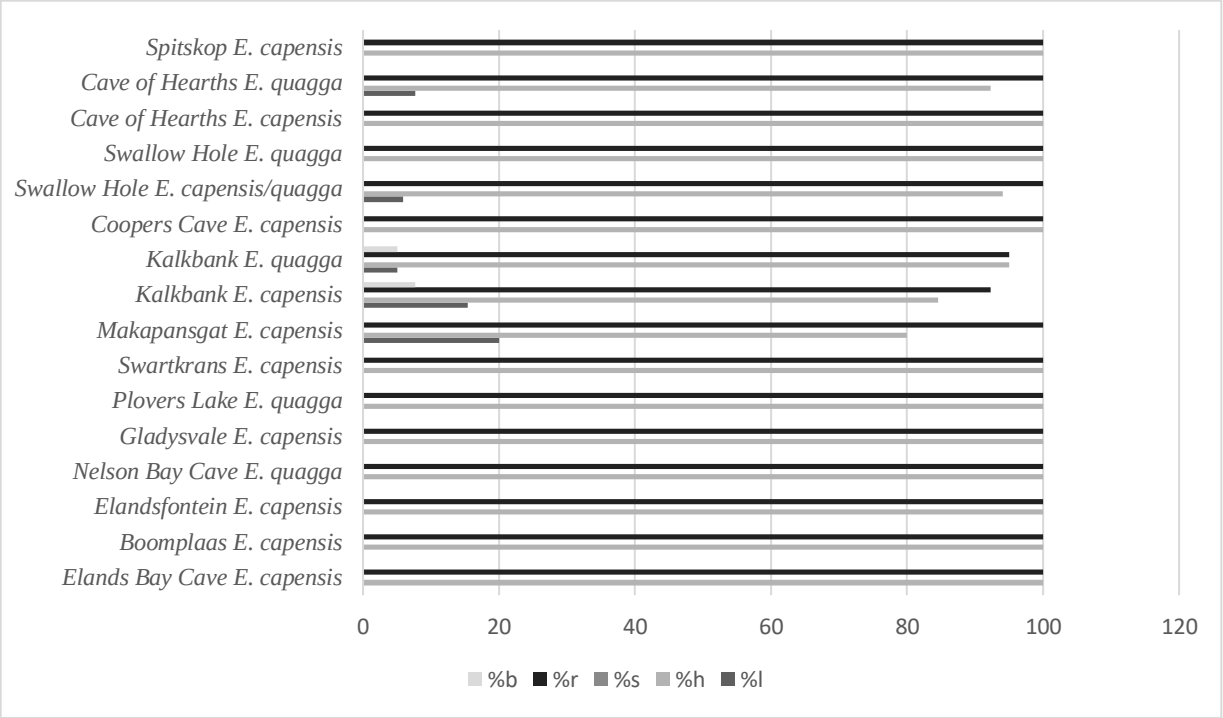


**Figure 4.4.2** Histograms comparing the mesowear patterns of *E. capensis* and *E. quagga* from various South African sites. %h=percentage high, %s=percentage sharp, %r=percentage round, %b=blunt, %l=percentage low.

not account for differences in terms of the grass type that is consumed (i.e. moist grass or not). Lastly, it is important to note that the modern *E. quagga* sample appears to be much more of an obligate grazer than those in the fossil sample, indicating that, although still grazers, the fossil

species was more likely (and/or able) to incorporate browse into its diet than extant plains zebras do today.

# Chapter Five

## Discussion and Conclusions

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### 5.1 Complications with the Historical Classification of *Equus capensis*

Taxonomic studies of long extinct fauna are typically problematic, largely due to the fragmentary and patchy nature of the fossil record. A lack of understanding regarding intra-specific variation in morphology within species can further complicate matters. Additional issues arise when there is an absence of information regarding the evolutionary history and distribution of taxa, leading to various species classifications being little more than hypotheses (Barraclough and Nee 2001). This has been particularly evident for classification of mammalian taxa in southern Africa over the last two decades; the issues surrounding nomenclature of fossil species has been largely ignored in favour of the taxonomist's desire to place new species names on record. As Bell (1950) questioned over half a century ago:

> "Is there any guiding principle in the application of taxonomy other than the battle-cry that distinguishable morphologic differences (all too frequently based on single specimens or single collections instead of on representative samples of populations) constitute specific differences? At present our taxonomy at the species (and generic) level expresses little except what apparently is a mad desire to create new names, and to emphasize that individuals are not alike" (Bell 1950: 496).

Even today, this desire to name new species, coupled with the lack of systematic review of African mammals, has led to naming a cornucopia of new species based only on the subjective description

of the taxonomist (Allmon 2016). Individual perceptions have greatly complicated attempts to determine taxonomies of controversial populations that are imperfectly represented in the fossil record, such as *Equus capensis*. There has been a considerable degree of oversplitting in equid nomenclature, and the biased nature of various species classifications has resulted in an incredibly complex and convoluted phylogenetic tree (Bennett 1980). Southern African equids in particular have been subject to this biased species naming process, and over time it has become clear that many of the assigned new species are in fact invalid and, more importantly, not based on rigorous systematic analysis (Haughton 1932, Bell 1950, Cooke 1950, Wells 1959, Churcher 1970).

### 5.1.1 Lower Dentition

*Equus capensis* is a primary example of a species of Perissodactyla from the Quaternary that was named from mandibular teeth (Broom 1909) with no systematic basis for doing so. It was originally considered a unique species on the basis of its large body size and apparently unique occlusal morphology of the lower cheek dentition. In later descriptions, Broom (1928) and others attempted further descriptions of the dental morphology of the *E. capensis* type specimen, as well as other specimens that had subsequently been assigned to this species. The chief issue with these descriptions is that various taxonomists described the morphology of *E. capensis* differently, resulting in contrasting opinions on where it might belong in equid phylogeny. Descriptions of occlusal morphology in general have been based on qualitative, individual assessments of shape, making geometric configurations unavailable for accurate comparisons between individual specimens or groups. At the same time, there has been a distinct lack of awareness of inter- and intraspecific variation in Equidae body size and dental occlusal enamel morphology. This is starkly illustrated in Broom's (1928) publication 'On some New Mammals from the Diamond Gravels of

the Kimberley District', where, based on nothing other than a comparison (by eye) of the differences between the *E. capensis* type specimen's teeth and other equid teeth found nearby, he reported a total of three new equid species, even suggesting that *E. capensis* may be a separate genus. No quantifiable reason was given for this.

With time, researchers began to realize that many of the species included in the South African fossil equid record had no biological basis. In a review of twenty equid species names, Wells (1959) determined that only six were actually definable. With regards to *E. capensis*, Wells (1959) determined that it should be deemed indeterminable (*nomina vana*) as its classification was based on damaged and incomplete lower teeth. Churcher (1970) disregarded Wells' (1959) assessment of *E. capensis*, claiming that it was in fact a determinable taxonomic entity that should also include fossils previously assigned to *E. hemlei*, *E. cawoodi*, *E. kuhni*, *E. zietsmani*, as well as some of the teeth that were referred to as *E. harrisi* and *E. plicatus*. It is important to note that Churcher's (1970) assessment of the taxonomic status of *E. capensis* is based on the type specimen, which is as previously mentioned, a mandible with fragmentary dentition. Ironically, it largely lacks occlusal enamel details, particularly around metastylid, metaconid and entoconid morphologies, as the occlusal areas were embedded in limestone. Broom (1928) represented the former two structures as rounded in his reconstruction, whereas Cooke (1950) depicted them as much more triangular in shape (Fig. 2.2.1). While GMM analysis of specimens assigned to *E. capensis* shows the dominant shape of metastylids and metaconids to be round (Fig. 4.1.5), there is still much variation within this feature. *Equus capensis* entoconids have been recorded as square (Churcher 2000), however analyses show both square and rounded entoconids. Hypoconids of *E. capensis* have been recorded as square (Churcher 2000), but again the GMM analysis points to a wide range

of possible shapes for this feature. Cooke (1950) also took issue with prior reasonings for naming the species, and introduced his own interpretation. He noted that Broom's (1928) illustrations of the type specimen were likely faulty due to its incompleteness. However, there is no reason for considering Cooke's (1950) rendering of the dental occlusal enamel as the correct one, particularly since he observed that the type specimen was likely even more damaged when he examined it. Clearly, the damaged and incomplete nature of the type specimen of *E. capensis* is problematic. Apart from large body size, a unique occlusal enamel pattern has been the basis for delineating *E. capensis* as a species distinct from other equids.

### 5.1.2 Upper Dentition

Since the type specimen did not include a maxilla or associated dentition, all large fossil equid upper teeth found in southern African Pleistocene deposits were historically classified as *E. capensis*, with no further reasoning beyond their size. Broom (1928) himself admitted that since only the lower teeth were known (and even then, not convincingly), his assignations at various times of large upper teeth to *E. capensis* may have been inaccurate. Similarly, Wells (1942) assigned worn upper teeth from the Witwatersrand collection measuring over 30mm in breadth to *E. capensis*. The result of assigning fossil equid upper molars to *E. capensis* purely on the basis of large size is evident in the current study where the GMM results exhibit a wide range of occlusal enamel patterns on teeth that are on average very large.

While the *E. capensis* type specimen does not preserve upper dentition, some authors have tried to reconstruct its maxillary occlusal enamel patterns based on unassociated large fossil teeth. Cooke (1950) and Churcher and Richardson (1978) suggested that the form of *E. capensis* maxillary teeth

are nearly identical to those of *E. quagga*, albeit larger. They noted that the hypoconal groove is deep, and the protocone is elongated and oval shaped. Observation of different examples of teeth assigned to *E. capensis* (Fig. 2.2.2), however, shows that this does not always hold true. The GMM analysis corroborates the observation (Fig. 4.1.6), showing variation in the protocone's shape as well as the depth of the hypoconal groove. Potts *et al.* (2018) stated that *E. capensis* does not in fact have as deep of a hyponocal groove as many other equids do, nor does it have an elongated protocone. There are clearly inconsistencies around which maxillary occlusal enamel characteristics are unique to *E. capensis*, if any. Churcher and Richardson (1978) further claimed that *E. capensis* has a very small protoloph, as well as a small hypocone. The GMM results again contradict this claim, exhibiting much more variation than historically acknowledged. Moreover, observation of a small subset of specimens assigned to *E. capensis* clearly shows that this is not always (or even most often) the case (Fig. 2.2.2, specimens C, D and F specifically). The two ectoloph halves are supposedly concave inwards within this species (Churcher and Richardson 1978), yet the maxillary morphospace for *E. capensis* specimens illustrate that this feature is quite variable. Recently, Potts *et al.* (2018) assigned two equid maxillary molars from Olorgesailie, East Africa, to '*Equus* aff. *capensis*' (the specimens are included in this research). The explanation for this allocation lies in the specimens supposedly having broader styles and more strongly developed pli caballine folds than *E. capensis*, but exhibiting the large size typical of *E. capensis* dentition. Pli caballine folds have been noted as undeveloped in *E. capensis* (Haughton 1932), however GMM analysis shows that this is not true for all specimens. The *E.* aff. *capensis* specimens are also noted as having less rounded protocones and deeper hypoconal grooves than *Equus capensis*. However, this is only according to authors' personal description of *E. capensis*.

The claims that *Equus capensis*' upper molars are essentially identical to that of *E. quagga*, but larger overall (Cooke 1950, Churcher and Richardson 1978), are, to an extent, in accordance with results from the maxillary GMM analysis (Fig 4.1.4). While there are clearly size differences between the *E. capensis* and *E. quagga* samples (Fig 4.1.8), there is no significant differentiation between the two with regards to occlusal enamel pattern. Although it is expected that variation within a single species' four cheek teeth will be present, it is assumed that there will still be broad level separation across species' patterns (Churcher 2000). This does not appear to be the case, and no idealized pattern of morphology distinguishes *E. capensis* from *E. quagga*, or any other equid species. These results confirm that large size and not dental enamel occlusal pattern was the main basis on which fossil equid teeth were assigned to *E. capensis* throughout history (and still is). Significantly, a species-specific dental size range has never been defined for *E. capensis*, which means that researchers have been subjectively assigning large fossil equid teeth to it. This has also caused uncertainty at localities where no obvious size groups are apparent. For example, in the Cave of Hearths assemblage, various specimens were classified as '*Equus capensis/quagga*' presumably because in the mind of the analysts, they could not be clearly allocated into one or the other taxon in terms of size. This uncertainty is apparent in the GMM results for this site (Fig. 4.1.11). Moreover, the same composite category was created at Elands Bay Cave for this same reason. It is clear from a survey of historical research and GMM analyses carried out in the current study, that there is much variation in morphological traits of teeth allocated to *E. capensis*, and an idealized occlusal enamel pattern as suggested by early researchers, does not exist. As a result of this, the concept of defining this species by way of occlusal enamel morphology falls away.

## 5.2 *Equus capensis* versus *Equus quagga*

### 5.2.1 Further Consideration of *E. capensis* and *E. quagga* Enamel Patterns

*Equus capensis* and *Equus quagga* are recorded as having occurred concurrently at almost all mid- to late Pleistocene sites in South Africa (Fig. 2.2.5). Researchers claimed to have used both occlusal enamel pattern (Broom 1928, Churcher 2000) and dental size (Churcher and Richardson 1978) when distinguishing the two from each other. However, because GMM analysis was unable to distinguish *E. capensis* from *E. quagga* on the basis of occlusal dental enamel pattern, it is likely that these researchers were basing their conclusions primarily on tooth size.

Morphological variability appears to be slightly higher in the maxillary teeth than mandibular ones, with mandibular teeth of both *E. capensis* and *E. quagga* clustering in a similar fashion to each other. This could also be the result of the smaller mandibular sample size. Importantly, both groups show variability in much the same way, with similar values along both RW1 and RW2. In the mandibular sample, 68% of *Equus capensis* teeth, and 67% of *Equus quagga* teeth, have positive RW1 values. If the two are discrete taxonomic entities, these results are surprising, especially considering the narrow and specific enamel pattern descriptions that have historically been provided for *E. capensis*' categorization. This type of variation is more indicative of closely related species or conspecifics.

That these two groups are both found at the same southern African sites and show no distinction in their occlusal enamel form (and are thus only separated by size), calls into question their species-level separation. Moreover, the maxillary specimens identified as *Equus capensis/quagga*, all cluster directly in between those identified as *E. capensis* and *E. quagga* for centroid size (Fig. 4.1.11). This further indicates the evident confusion that surrounds classifying this large zebra,

since when the size discrepancy is not inherently obvious and is somewhat intermediate, specimen classification can go either way.

### 5.2.2 Homogenous Enamel Complexity in *E. capensis* and *E. quagga*

OEI analysis was conducted on the dentition of both *E. capensis* and *E. quagga* samples. OEI relates to phylogeny; it is a morphological signal of an animal's genetics. Hence, the analysis was performed under the impression that, should these be two distinct species, the complexity of the enamel will perhaps highlight what GMM did not. However, complexity analysis indicates much the same thing as shape analysis – these supposedly discrete species are scarcely separated (Fig. 4.3.1). If *E. capensis* and *E. quagga* are separate evolutionary entities, presumably their enamel complexity would differ considerably, especially given their difference in size (Famoso *et al.* 2013). Having greater complexity is an adaptation for persistence in more xeric environments, so, because *E. capensis* is notably large and disappeared at the Pleistocene-Holocene transition, if it was a discrete taxonomic unit it would be expected to have considerably more complexity. Although *E. capensis* shows overall slightly higher levels of complexity than *E. quagga* (the difference between medians is 0.482), this difference is not significant. Added to this, out of the six equid groups analyzed, *E. capensis* is the most similar in enamel complexity to fossil *E. quagga*. *Equus capensis* has been noted as the most similar in size to *E. grevyi* (Churcher 2006, Faith *et al.* 2013). Thus, *E. capensis* being more closely associated to *E. quagga* in complexity is even more interesting. Perhaps even more telling of their overall close interrelatedness, the *E. capensis* and fossil *E. quagga* samples are also more similar to each other than fossil *E. quagga* is to extant *E. quagga*. As is the case in the GMM analysis, the complexity of *E. capensis* occlusal enamel is indistinguishable from that of the *E. quagga* specimens. That the results of both methods

are in agreement leads to further doubt on the reasoning behind separating *E. capensis* and *E. quagga* into distinct taxonomic entities. Systematically, the two are indistinct in form as well as complexity, and they do not exhibit any taxonomic characteristics proven by these methods to support them being distinct species. In light of the above results, it could be postulated that *E. capensis* and *E. quagga* are conspecific with the former representing a larger morphotype of the latter. This is evidence is supported by the skull proportions of *E. capensis* which reveal additional morphological similarities to *E. quagga* (Eisenmann 2000, Orlando *et al.* 2009). Within extant equid taxa, dental occlusal enamel pattern strongly separates clades, and further separates species (Cucchi *et al.* 2017).

The results of this study are largely consistent with aDNA evidence that suggests that *E. capensis* formed a clade within the extant plains zebra group, clustering amongst the historically extinct quagga and extant plains zebra (*E. quagga*) (Orlando *et al*. 2009, Faith 2014). Because of this, Orlando *et al.* (2009) do not consider *E. capensis* to be a separate species or even subspecies of *E. quagga*.

### 5.2.3 Phenotypic Plasticity in *Equus quagga*

If indeed *E. capensis* and *E. quagga* are the same species, we need to further account for the large size of the former. The extant *E. quagga* is a geographically dispersed, phenotypically plastic zebra species (Lorenzen *et al.* 2008). Based on the mutation rates of mtDNA, it appeared roughly 1 million years ago. Since then, its development was shaped by Pleistocene climatic and environmental fluctuations (Lorenzen *et al*. 2008).

Extremes in resource availability are known to produce adaptive extremes in phenotypic variability in large mammals such as equids (Geist 1989). Change in climate, and the associated impact on factors like humidity and temperature, is universally recognized as the principal driver of phenotypic variation (Jones 2012). The more heterogenous the climate, as in the mid-to late Pleistocene, the more favoured and persistent phenotypic plasticity will be (Searle *et al.* 2009). The higher the degree of plasticity, the higher the chances of a species' long-term survival. *Equus quagga* is one of the longest lived species of equid, surviving the tumultuous Pleistocene epoch and obtaining a historical range unmatched by any other living African equid (Fig. 2.1.4). Thus, it makes sense that the species shows such high levels of phenotypic variation.

One of the chief differences between extant geographical populations comes in the form of striping – *Equus quagga* in northeastern Africa are fully and boldly striped, whereas the southernmost variants display reduced striping and a much lower contrast between stripe colours (Herries and Bell 2004, Reynolds 2005). There is also morphological variation in their dentition, with the presence of infundibula on the lower incisors in the northmost populations, but not the southern ones (Groves and Bell 2004). Lastly, the southern African *E. quagga* is significantly larger than its counterparts living further north. Six regional subspecies were previously assigned to the plains zebra based on varying morphologies. However, DNA studies have since indicated that all regional populations lacked the genetic structure that would deem them discrete evolutionary units (Lorenzen *et al.* 2008, Orlando *et al*. 2009). The six subspecies assignments have since been withdrawn.

In mammals, phenotypic plasticity is arguably most often demonstrated by changes in body size,

as this characteristic is more affected by the environment than many other genetically underpinned factors (Brown and Brown 1992, Hutson and Wolverton 2011). Exploring size plasticity in mammals allows one to determine the effect of environment rather than genetics on the development of an organism, and by extension to discriminate between genetic effects and environmental/climatic effects (Geist 1989). In *E. quagga*, mitochondrial as well as nuclear DNA show high levels of genetic exchange across vast areas. The species further demonstrates great plasticity, and thus a strong capability to recover and respond to varying conditions via this plasticity (Lorenzen *et al.* 2008).

### 5.3 Body Size Differences Correlated with Pleistocene Climatic Fluctuations

Ancient DNA evidence has shown that *E. capensis* is genetically similar to *E. quagga*, and in this study, I have shown that its premolars and molars are indistinct from those of *E. quagga* with regards to overall occlusal shape and occlusal enamel pattern. These results challenge the long held belief amongst palaeontologists that *E. capensis* was a unique zebra species that went extinct at the end of the Pleistocene. If it was not a distinct species but an extinct morphotype of *E. quagga* as suggested by aDNA and dental morphology, how does one explain its large size compared to *E. quagga* and also, fossil evidence suggesting that it co-occurred with *E. quagga* throughout the Pleistocene?

It is recognized that some phenotypic adaptations are ecological responses to changes in climate (Geist 1989, Ozgul *et al.* 2009), and that these are not necessarily processes of evolution. Studies of phenotypic change have oftentimes focused on genetic responses to selection, however genetics does not always explain phenotypic outcomes (Brown and Brown 1992, Ozgul *et al.* 2009). In

these cases perhaps, the plastic responses seen in many mammalian lineages are caused by climatic/environmental factors. It is evident that there is an array of species-specific responses to fluctuating climates, one of the most prominent of which (and one that has been observed in a variety of different species) is a change in body size. Individuals within certain species oftentimes vary in their mean size, and the primary suggestion provided to explain this observation is a response to differing temperatures (Avery 1982). The dynamics of body size within a species have more recently been explained as a consequence of climatic variation rather than genetic evolution (Brown and Brown 1992, Ozgul *et al.* 2009). Various studies have shown that there is a relationship between size changes in fossil mammals and changes in paleoclimates from various parts of the world (Dayan *et al.* 1991). At the Pleistocene-Holocene transition in particular, a decrease in species body size is observed and is generally interpreted as triggered by the onset of global climatic warming (Davis 1981, Forsten 1993). It appears as though changes in body size should, instead of being interpreted as genetic evolution, rather be regarded as one of several strategies by which an animal is able to adjust phenotypically to different temperatures (Davis 1981, Geist 1989). A key modern example of environment rather than heredity determining an animal's morphology centers on the extant red deer (*Cervus elaphus*) (Geist 1989). This variable species is able to rapidly adapt its phenotype to suit local conditions when relocated to new environments.

### 5.3.1 Bergmann's Rule

Bergmann (1847) first proposed that significantly larger members of the same species will be found in cooler climates, and smaller members in warmer ones. The rule originally relied upon the relationship between latitude and body size, where latitude is a proxy for temperature (Bergmann

1847). However, this has since proved to be less accurate than the more recent reformulations of the rule. These state that intraspecific size variation is caused more by temperature and moisture than it is by latitude – small morphotypes are linked with hot and humid settings, and larger morphotypes with colder and drier ones (Dayan *et al.* 1991). The original rule also states that the reason for the size differences lies in heat conservation, another facet that has since been refuted by some scholars (Ashton *et al*. 2000). Lastly, Bergmann (1847) originally claimed that the rule was followed more habitually in smaller animals, however Freckleton *et al.* (2003) conducted a study and discovered that the trend is actually followed more commonly by larger species. Despite these glitches, the empirical validity of the rule still stands, even if its original explanation and some of the finer details have since been regarded as invalid (Ashton *et al.* 2000, Hutson and Wolverton 2011). This distinction is important because the empirical evidence for the rule is not unsound simply because the original explanation for it may be, and much of the debate surrounding it has nothing to do with observed intraspecific phenotypic plasticity (Hutson and Wolverton 2011).

Despite the speculation and arguments against Bergmann's Rule, it has been found to apply to a variety of animal lineages. Although the extent to which temperature will affect animal size does vary within and between species, experimental evidence has regularly suggested that higher temperatures can reduce the overall size as well as growth rate in an array of species, and that lower temperatures have the opposite effect (Sheridan and Bickford 2011). It is not possible to discuss a direct and undeviating link between climate, genotype and phenotype as all animals respond to climatic changes in unique and complex ways (Ozgul *et al.* 2009), but this does not mean that a link is not unmistakably present. A well-observed realization of this rule is seen at the

Pleistocene-Holocene transition. Because the period is characterised by rapid warming, it is unsurprising that there is an abundance of evidence for diminution of animals around this time. A rise in temperatures in Israel around 12 ka led to the majority of large mammals becoming smaller (Davis 1981). Modern animal populations in Israel were then also assessed, and interestingly the same pattern was shown with a reverse trend – species of boar, foxes and wolves (each demonstrative of different ecologies) all increased in body size as the temperature decreased (Davis 1981). Moreover, all three species increased in size in much the same way, where the regression lines of dental size (used as a proxy for body size) on temperature were analogous (Davis 1981).

Further evidence for size reduction at the terminal Pleistocene exists in southern African species as well. The greater red musk shrew (*Crocidura flavescens*) appeared to be larger in the Late Pleistocene – specifically between 25 ka BP and 14 ka BP – than in the Holocene (Avery 1982). The shrew showed size variation within the same area but during different periods in the past, and it is evident that there is a connection between large body size and the Last Glacial Maximum (LGM). Because of this, Avery (1982) hypothesized that the postglacial layers would comprise an overall smaller-bodied shrew – fauna from both Boomplaas and Byneskranskop expressed rapid change over stages of a few hundred years, with smaller mean body sizes in younger and consequently warmer levels. Also in southern Africa, Klein (1975) found that the Cape grysbok (*Raphicerus melanotis*) was significantly larger during the colder stages in the Cape Biotic Zone. Seventeen southern African carnivore species were also analysed to establish if they were larger in cooler climates and thus conformed to Bergmann's rule (Klein 1986). In fourteen of the species studied, mean size within the same species was shown to be greater in the fossil samples which

accumulated under comparatively cooler conditions (Klein 1986). Brink (2005) also noticed an interesting pattern in black wildebeest (*Connochaetes gnou*), where populations experienced changes in body size through time, though not at a constant tempo. Central interior populations (generally warmer than the coast) underwent a reduction in size within the last 5000 years, and those along the southwestern coast of South Africa were shown to be more robust than contemporary specimens in the central interior (Brink 2005). Added to this, the larger daughter populations occurring along the southern coasts disappeared at the terminal Pleistocene.

The disappearance of the giant African buffalo, *Syncerus antiquus* (formerly *Pelorovis antiquus*), during the Late Pleistocene-Holocene period in southern Africa is another interesting case. Besides larger body size and unique horn shape, little else separates *Syncerus antiquus* from *Syncerus caffer* (Peters *et al*. 1992, Klein 1994). This raises questions around the status of *S. antiquus*. Was it merely a Pleistocene version of *S. caffer* or were the two discrete species (Peters *et al.* 1992)? It is noted that if they were not within the same chronospecies, and the modern *S. caffer* is a representation of phyletic change, then there should be more distinctive morphological differences between the two than what there is (Peters *et al.* 1992). Peters *et al.* (1992) have suggested that the larger size of *S. antiquus* was an adaptation to the cold, arid, grassy environment of the Pleistocene, while *S. caffer*'s smaller size was an adaptation to warmer conditions and a reduction in grass cover during the Holocene interglacial. It is acknowledged that the two are difficult to discern postcranially or dentally (Klein 1994), but that their geographic and temporal overlap is cause for separating the two taxonomically. However, there are known issues when it comes to reconstructing the chronometric data of southern African sites, as there is little geochronological regulation and by extension, difficulties in determining accurately which fossils occurred in which

horizons in time (Carrión *et al.* 2000, Chase and Meadows 2007). Therefore, *S. antiquus* and *S. caffer* may well not have been contemporaneous at all.

### 5.3.2 The Impact of Bergmann's Rule on Equids

In East as well as South Africa, various mid-Pleistocene species possessed large body size, as well as dental traits that indicate a preference for large quantities of fibrous grasses (Potts and Deino 1995). In studies of European fossil horses, it was found that an increase in tooth size during the Pleistocene was an adaptation to arid conditions and abundantly available abrasive plant foods (Eronen *et al.* 2010). That these adaptive qualities are present in equids necessitates consideration of the role that climate and environment played in their eventual extinctions. The beginning of the Holocene was distinguished by an increase in temperature as well as rainfall, altering heat levels and arid grass availability (Faith *et al.* 2013). This consequently resulted in widespread replacement of arid-adapted grazing equids with moist-grass grazing equids.

The mammalian fossil record shows that equids are amongst the wealth of mammals where body size has been influenced by climate. More specifically, they have been shown to conform to Bergmann's Rule, observed mainly at the Pleistocene-Holocene transition. While the ability to be phenotypically plastic and foster large body size is demonstrably advantageous, especially during periods of climatic fluctuations, there are vulnerabilities that accompany this flexibility. A large herbivorous mammal must continuously feed, and thus needs a large area of land for it to be nutritionally sustained (Coe 1982). Comparatively, a larger herbivore will exploit an abundant amount of low quality food, while a smaller one will consume less food but of a higher quality (Kleynhans *et al*. 2011). This trend is followed by extant zebras, where larger zebras occupy more

open habitats with savanna-typical vegetation, and smaller zebras typically prefer more wooded habitats (Alberdi *et al.* 1995). Added to this, populations of larger animals generally have longer gestation periods, leading to slower population turnovers (Coe 1982). Since smaller individuals are able to survive on less despite requiring higher quality grasses, and coupled with their shorter gestation times, it is not surprising that larger individuals are generally the ones that suffer the most during periods of climatic change, specifically those accompanied by warming. Because body size is so closely related to these environmental constituents that affect resource availability, the ecological preferences of fossil animals of known body size may be surmised (Alberdi *et al.* 1995).

Caballoid horses from an array of mid-to late Pleistocene sites in Europe were analysed, and it was found that in the Late Pleistocene, populations of large horses petered out, either decreasing in size or being replaced by medium-sized morphotypes, ultimately becoming extinct at the commencement of the Holocene (Forsten 1991b). The population of small horses, however, continued on in the Holocene. Evidently a decrease in size occurred in European caballoid horses, but more abruptly in the Late Pleistocene (Forsten 1991b). Further north in Alaska during the Pleistocene, many size variants of horses emerged, and while new forms continued to appear through time, the larger variants continued to fall out (Guthrie 2003). It has been shown that these Pleistocene horses too experienced a general decline in body size, and that this is best attributed to the climatic shifts of the time (Guthrie 2003). It is suggested that the large horses in Alaska were the most prosperous during the LGM, and were also the first species in the area to disappear at the beginning of the Holocene. They were specialized grassland-dependent grazers, and the observed

size decrease of these fossil horses during this time is credited with a shift towards more mesic environments and overall climatic warming (Guthrie 2003).

### 5.3.3 *Equus quagga* and Bergmann's Rule in the Pleistocene

Extant *E. quagga,* as mentioned, is a plastic species with the widest known range in living equids, extending all the way from South Africa; north to southeastern Sudan, southern Ethiopia and southern Somalia (Groves and Bell 2004, Faith *et al.* 2013). Across this range, there exist strongly distinct phenotypes within the species, chiefly separated over the northeastern and southern populations (Groves and Bell 2004, Reynolds 2005). While these differences, discussed above, include striping patterns and incisor variation, it must be emphasized that the primary phenotypic difference amongst plains zebras is in their overall size. Morphometric analyses have illustrated cranial as well as dental dimensions to be much larger in southern African plains zebras than East African ones (Reynolds 2005). The disparity in size illustrates that this feature is one that they have great capability of altering. This significant difference in size is likely related to the divergent climates of East and South Africa, with the southern range being colder. These various trait differences lie behind the reason that regional *E. quagga* populations were previously assigned subspecific statuses. Despite an array of physical dissimilarities between regional populations, genetic evidence proves that the plains zebra is in fact a single species that possesses the ability to adapt its phenotype in a host of ways, that includes size.

*Equus quagga* endured recurrent glacial/interglacial fluctuations during the mid-to late Pleistocene. Given its plasticity as a species, it's persistence into the present must have been facilitated by dramatic shifts in phenotype. During the surprisingly long glacial cycles that

characterized the latter half of the Pleistocene, average body size in *E. quagga*, like other mammals of the time, must have increased to withstand colder climatic conditions and take advantage of the increased abundance of grass. The results of this study suggest that *E. capensis* was the larger glacial-adapted morphotype of *E. quagga*. With the onset of interglacial periods, mean body size would have begun to revert back to the smaller morphotype, recognized as *E. quagga* in the fossil record, to be able to survive the warmer climatic conditions and more varied plant community. This smaller and ecologically adaptable morphotype of *E. quagga* survived into the Holocene while *E. capensis* disappeared.

### 5.4 Addressing the question of conspecificity

In light of the results of this study, how does one explain the long-held belief amongst palaeo-scientists that *E. capensis* and *E. quagga* not only co-occurred, but formed mixed herds (Churcher 2014) throughout their range? Firstly, it is questionable on ecological grounds that the two actually co-existed. Two morphologically and behaviourally similar species generally cannot coexist in a single locality if they overlap significantly in ecology (Gingerich 1974, Pfennig and Pfennig 2009), thus the assumed co-occurrence of *E. quagga* and *E. capensis* is incongruous. The distribution patterns of extant zebras (Matthee *et al.* 2004, Moodley and Harley 2006) also call into question the suggestion that *E. quagga* and *E. capensis* co-existed. Competitive exclusion is known to be one of the chief factors in the dispersal of modern zebra species (Schulz 2012). Extant southern African zebra species barely overlap, and each tend to have their specific home range (Estes 1991, Matthee *et al.* 2004).

If *E. capensis* and *E. quagga* were indeed separate species and overlapped, the only feasible

ecological explanation would be character displacement. Character displacement assumes that closely-related species must partition resources in order to co-exist, and that this divergence predominantly takes the form of a differentiation in size (Dayan and Simberloff 2005). However, despite the overall size differences between *E. capensis* and *E. quagga* (Figs. 4.2.1 and 4.2.2), the likelihood of character displacement and resource partitioning is low. Firstly, the sole purpose of developing size differences in these instances is to reduce overlap in resource use (Dayan and Simberloff 2005), as intraspecific competition for resources has long been viewed as a leading cause for character displacement (Pfennig and Pfennig 2009). Yet, despite the size difference between them, mesowear evidence suggest that *E. capensis* and *E. quagga* still made use of similar resources i.e. both were obligatory grazers (Fig. 4.4.1). Moreover, OEI results signify adaptations for an equally abrasive diet in terms of the complexity of their enamel (Fig. 4.3.1). Character displacement must therefore be ruled out.

### 5.4.1 Fossil evidence of co-occurrence?

While it is ecologically unlikely that *E. capensis* and *E. quagga* could have co-existed, how does one explain the co-occurrence of their fossilized remains at several sites? The sites that produced both *E. capensis* and *E. quagga* fossil material are either open localities with little or no stratigraphic integrity, or have complicated stratigraphic sequences that have not been clearly defined (discussed in Chapter 2 and individually in appendix A).

A primary example is Elandsfontein, where the majority of materials collected were done so unsystematically, disregarding associations and spatial relationships (Klein 1988). The stratigraphy of the site is difficult to interpret, and it has simply been the assumption that all closely

associated bones and artifacts at the site are penecontemporaneous (Klein 1988). Teeth assigned to *E. capensis* and *E. quagga* are well represented at the site, however it is not possible to claim that they co-occurred given the lack of clear stratigraphic and dating information. Another site at which this is an issue is Vlakkraal. Here, both zebra types are represented, albeit with no systematic excavations or stratigraphic definitions provided. Kalkbank contains an abundance of *E. capensis* and *E. quagga* material, again though with no delineated stratigraphy or reliable dates available (Hutson 2006, Hutson and Cain 2008). The fossils from Cave of Hearths come from mixed deposits, similarly creating difficulties in attempts to separate the *E. capensis* and *E. quagga* material (Klein 1988). Gladysvale is a cave site where the decalcified sediments shows no clear stratigraphy, and the *E. capensis* fossils are noted as having been moved out of their original context anyway. Cave sites such as Byneskranskop and Nelson Bay Cave have suffered mixture of materials and disruption of layers, as demonstrated by inversions of the dates obtained for both these sites (Schweitzer and Wilson 1978, Loftus *et al.* 2016). Boomplaas cave is noted as having good stratigraphic integrity, yet also presents inverted dates across layers (Pargeter *et al.* 2018), pointing to bones having moved down the sequence. Additionally, separating closely related species from the site proved challenging and many (including *E. quagga*) were thus compounded in processes of categorization (Klein 1978). There is no sequential variability offered for these sites, the result of which is the diversity of the collective fossil species appearing higher than what actually existed during a given time period (Peterson 1977). Clearly, the suggestion that *E. capensis* and *E. quagga* co-existed is not based on undisputable stratigraphic or dated evidence. One can thus not discount the possibility that they represent morphotypes of the same species that occurred alternately on the landscape in response to climatic fluctuations during the mid-to late Pleistocene. Based on this possibility, discounting sexual dimorphism as an alternative option must

again be emphasized. As discussed earlier, a study by Seetah *et al.* (2014) determined that sexual dimorphism is not present in horse check teeth and does not complicate discernment of horse populations. Added to this, a study was conducted whereby extant horses across a variety of species and breeds were analysed for intraspecific sex and age variation, via size and shape of cheek teeth and other skeletal elements (Van Asperen 2013). This was done in order to test if differences between sexes may affect analyses of variation in inter- and intraspecific late Middle Pleistocene horses from northwest Europe. Results indicated that the fossil horse assemblage was equally as variable as the modern sample of many different breeds. This suggests that the variation between samples from differently dated stages of the Middle Pleistocene can rather be considered as intraspecific variation; which is the result of ecomorphological adaptation to the fluctuating climate of the Pleistocene (Van Asperen 2013). It is concluded that in Pleistocene equid assemblages such as those included in this research, which represent a considerable and often averaged length of time, the changes in size over time are more significant than changes in size between sexes (Van Asperen 2013).

### 5.5 Future research

As mentioned, the issue of *E. capensis* occurring contemporaneously with *E. quagga* is greatly confounded by the lack of temporal resolution at all sites in which they are both present. Based on both modern comparisons and the fossil record, their co-occurrence is unlikely but has yet to be resolved with exact dates. Thus, a more decisive way to determine that this was the case would be to directly date fossil teeth from each assigned species from the same locality, and to repeat this across various sites.

Future research should also explore the accuracy of the novel GMM protocol for equid maxillary cheek teeth introduced in this study. While traditional landmark analysis has previously been conducted on equid maxillary dentition and has been shown to be accurate, combined traditional and semi-landmarks have not been applied until now. In order to corroborate the results produced via this method in the current research, it should be repeated using the same criteria in order to confirm its precision**.**

Lastly, it would be useful to perform additional aDNA analyses on assigned *E. capensis* dental material. The previous aDNA study of *E. capensis* was conducted on just a handful (*N*=4) of specimens from a single locality. Therefore, it would be valuable to test a variety of dental specimens that come from different sites, are different sizes, and have different presumed ages. While the study by Orlando *et al.* (2009) is suggestive of a close relationship between *E. capensis* and *E. quagga,* their results can only be confirmed once a large, temporally and geographically diverse sample has been analysed.

## 5.6 Potential Limitations

### 5.6.1 GMM Protocol for Upper Dentition

The method for quantifying the occlusal enamel pattern of mandibular equid teeth was established and proven by Cucchi *et al.* (2017), so this protocol was followed for analyses of lower dentition. However, there is currently no existing protocol for the analysis of occlusal enamel patterns in maxillary equid teeth that encompasses traditional as well as sliding semi-landmarks. For this reason, I created a protocol based on the mandibular blueprint of that set forth by Cucchi *et al.* (2017). Because this particular method has not yet been repeated or tested empirically, it is possible

that there are inaccuracies. The chief potential for error or missed information lies in the arrangement of occlusal enamel patterning in upper equid teeth. In mandibular dentition, there is one continuous enamel pattern that can be traced around the outer part of the occlusal surface. Maxillary dentition, on the other hand, contain this same type of bordering enamel pattern, but also include the prefossette and postfossette (Fig. 3.2.4) in the centre of the enamel. These inner enamel patterns were not quantified, and it is possible that there is taxonomic variation in these features.

### 5.6.2 No Distinction Between P3 – M2

Teeth in the fossil record are almost always found in isolation, and discriminating between the middle four cheek teeth is nearly impossible when the others are not available for comparison. This is especially problematic for extinct species where nothing is known about intra-specific variation in cheek tooth patterns or intra-tooth variation. Because of this, P3 – M2/p3 – m2 were not analysed in separate groups in GMM analyses, and were all categorized under one tooth type. Where possible (when more than one cheek tooth was available for analysis) M2/p4 was used, however, instances of this were rare. It has been noted that there is slight morphological variation between the four cheek teeth (Churcher 2000), although it is assumed that this intraspecific variation is not significant compared to interspecific morphological discrepancies that is evidenced across species. Related to this, the sample size could affect the patterns of variation observed within species, as the type of cheek tooth was typically not known.

### 5.6.3 Tooth Size as a Proxy for Body Size

One must be cautious when attempting to determine the body size of fossil mammals. Body size prediction equations are typically grounded in extant taxa (Anyonge 1993, Delson *et al.* 2000), leaving room for error when applied to fossil samples. Additionally, estimates usually come from measurements of only one anatomical region, and while there is no concrete solution for which anatomical region is the best suited (Dagosto and Terranova 1992), a combination of variables will likely yield better results. However, this type of variety is not typically available in the fossil record. A mammal's tooth size and growth are diet/environment dependent, where the size of teeth are important indicators of dental function. Because overall tooth size is less genetically driven, limb bones have since been recognized as perhaps better indicators for body size estimates (Bergqvist 2003). However, because of their identifiability and great preservability, teeth will always be used by palaeontologists as proxies for body size. *Equus capensis* has very few postcranial elements assigned to it, so it is also challenging to know whether this is the result of these elements being smaller in comparison to dental assignments and they have thus predominantly been assigned to *E. quagga*, or if there have simply not been enough limb elements recovered.

## 5.7 Conclusions

The results of this study call into question the taxonomic validity of *E. capensis*. Analyses of teeth assigned to it fail to reveal a common occlusal enamel pattern. Also, the occlusal enamel patterns of these teeth are not unique, as they are shared with a variety of other equids, both extinct and extant. On the other hand, teeth in the *E. capensis* sample are on average larger than those of other equids with which they were compared. While this is consistent with past and currently-held opinion that *E. capensis* was a distinct large-bodied equid species, body size in mammals is not a

sound indicator of taxonomic distinctiveness as it is strongly influenced by climate and environmental factors.

The conclusions of this study are consistent with available aDNA evidence that suggests that *E. capensis* was an extinct morphotype of the extant plains zebra *E. quagga*. If this was indeed the case, its large body size might have been an adaptation to prolonged glacial climatic and environmental conditions typical of the mid-to late Pleistocene. There is little secure evidence to support the currently-held belief that *E. capensis* and *E. quagga* were two distinct but contemporaneous equid species that shared the Pleistocene landscape. Rather, given the current evidence, a more parsimonious scenario would entail the two existing at different times during the Pleistocene, with *E. capensis* representing the glacially-adapted, and the smaller-bodied fossil *E. quagga* representing the interglacially-adapted morphotypes of the same species, represented today by the extant *E. quagga*.

The results of this study has implications for other well-known fossil species that have become entrenched in palaeontology, many of which were also named in the early 20$^{th}$ century. Despite the possibility that these species may also not be taxonomically valid, researchers have continued to refer to them without question. With a more comprehensive understanding of intra-specific variation, modern scientists are compelled to investigate questionable fossil taxa so that we do not build on previous mistakes. A failure to do so will thwart progress in the field, or worse, lead us off track.

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# Appendices

## Appendix A

### Palaeontological Contexts of the Studied *Equus* Dental Material

The following is a brief breakdown of all South African sites included in this research. All equid material included in this study are derived from these sites. A summary is provided for where the sites are located, the context of the given site, its excavation history, particulars on the faunal recovery where pertinent, and details of the various techniques employed to date the sites. Also briefly mentioned are, where applicable, issues of discontinuity and potential errors in site ages.

1. Vlakraal

Vlakkraal is located north-west of Bloemfontein, in the Free State province (Wells *et al.* 1942). It consists of several thermal springs, one of which is fossil-bearing despite being an unstratified accumulation of spring debris (Wells *et al.* 1942). This is where the *Equus capensis* material comes from. None of the springs have been systematically excavated or stratigraphically defined. They have also not been formally dated; however, the presence of Middle Stone Age (MSA) lithic material suggest that the Vlakkraal springs are Late Pleistocene in age (Ecker and Lee-Thorp 2018). Additionally, the Vlakkraal faunal remains (including teeth of three species of *Equus*, one of which was identified as *E. capensis* based on its large size) have never been described, but were assumed to be contemporaneous with the Florisbad faunal assemblage due to its close proximity to that locality.

2. Spitskop A (Senekal)

This site is located north-east of Groblersdal, in Limpopo province, and consists of a river that flows through the centre of the complex (Harmer 1992). A basin has been sculpted by this river, and forms the units of the Spitskop Complex. There is no information on how the site was originally excavated, and it has only been dated to the Late Pleistocene based on associated Late Stone Age (LSA) technological assemblages (Ecker and Lee-Thorp 2018).

3. Equus Cave

Equus Cave is situated near Taung in the southern Kalahari. Brown hyenas (*Parahyaena brunnea*) have been implicated as the accumulators of the wealth of fossil material found at the site (Scott 1987, Klein *et al.* 1989). The stratigraphic units have been noted as poorly defined, and prior to the site's initial excavation, the cave that contained it was partially destroyed as a result of commercial quarrying (Klein *et al.* 1989). Pollen sequences from the site have been studied and demonstrate changes in climate from wetter conditions in the Late Pleistocene to dryer conditions in the Holocene (Scott 1987). Many of the radiocarbon dates for the site are out of stratigraphic order, perhaps due to unreliable radiocarbon ages on the dated materials (Johnson *et al.* 1997). Nevertheless, radiocarbon ages range roughly from 10 000 BP to 28 000 BP (Johnson *et al.* 1997; Ecker and Lee-Thorp 2018).

4. Coopers D Cave

Coopers D is located north-west of Johannesburg, between the well-known sites of Kromdraai and Sterkfontein (Berger *et al.* 2003). Uranium-Lead (U-Pb) dating of speleothems underlying the entire site have produced dates of 1.5 Ma - 1.4 Ma (de Ruiter *et al.* 2009). Correlations between the fauna at Coopers D with assemblages from the abovementioned nearby sites, have suggested

an age of between 1.6 and 1.9 Ma (Berger *et al.* 2003). There are two distinct episodes of fill that are observable within the stratigraphy, and the deposits here are found in dolomites (Berger *et al.* 2003). Despite the apparent division of stratigraphy, there are no clear differences between the recovered fauna from either layer. Equid specimens are rare at the site, and only two taxa have been identified – *E. quagga* and *E. capensis*.

5. Buffalo Cave

Buffalo Cave is located at the base of a cliff in the Makapan Valley, Limpopo province. Most of the fossil material derived from this site were originally encased in breccia blocks that were out of context as a result of mining (Kuykendall and McKee 1995). Complicating matters further, some of the fossil material had been redistributed by water (Herries *et al.* 2006). Since the majority of the recovered faunal remains are incomplete/embedded in the breccia, taxonomic identification has been difficult, and most could only be assigned to genera. Palaeomagnetic dating has been conducted on *in situ* blocks, and the fossil-bearing segment of the site has been assigned an age of 1.07 Ma - 780 ka (Herries *et al.* 2006). Palaeomagnetism has been applied to a variety of nearby sites in the Makapan area and has often seen contradictory results, with no clear cut absolute dates achieved (Herries *et al.* 2006). As such, it has proved extremely difficult to concretely place the fauna within a confirmed chronological sequence.

6. Elands Bay Cave

This well-known cave site is located on the west coast of South Africa. The bulk of the excavations at the site took place in the 1970s, with a considerable amount of faunal remains uncovered (Sillen and Parkington 1996). Systematic excavations in combination with a thorough set of dates, suggest

a pulsed occupational history for the site, where periods of regular use are interspersed with no occupation at all (Sillen and Parkington 1996). The cave has been dated to >40 000 - 300 BP (Cartwright and Parkington 1997) based on around 60 radiocarbon dates obtained from wood charcoal deposits. However, it has been stated that there were earlier periods of occupation that are beyond the range for $^{14}C$ dating. Added to this, the charcoal assemblages have been used for palaeoenvironmental reconstruction, where it is noted that many of the animal taxa found in these assemblages are widely distributed and tolerant of a range of environments (Cowling *et al.* 1999). The equid material (consisting only of *E. capensis* and *E. quagga*) was recovered from the layers dating to around 13 600 BP, during the LGM, and is absent at the onset of the Holocene around 10 000 BP (Klein and Cruz-Uribe 2016). Interestingly, Klein and Cruz-Uribe (2016) note that some of the equid teeth were assigned to a composite category including both species, as they were difficult to distinguish between.

7. Elandsfontein

This site is located inland of the Atlantic shoreline in the Western Cape province. It is an extensive open site located in an active dunefield (Braun *et al.* 2013). The first collections of material took place in the 1950s and 1960s, and almost all of what was retrieved was done so unsystematically from deflation surfaces between dune plumes (Klein *et al.* 2007). These early occasional material collections conducted at the site were predominantly unfruitful. Because of this, reconstruction of context has been largely unviable. Later, between 2008 and 2012, more systematic excavations were carried out in the deflation surfaces, where faunal collections are said to be *in situ*, or at least near their original place of deposition (Braun *et al.* 2013). It is thought that these fossils suffered little post-depositional disturbance, and thus the lithologies' relationship to the stratigraphy and to the fossil occurrences may be inferred (Braun *et al.* 2013). Dating of the site has been complicated,

since direct dating of fauna is impossible and almost all collected material are *ex situ*. Added to this, it is difficult to date the sand as it is continually moving. Based on the taxonomic composition of the occurring fauna, together with comparisons to dated faunas in East Africa, the site has been assigned a broad age of 1Ma - 600ka (Klein *et al.* 2007, Braun *et al*. 2013, Lehmann *et al.* 2016).

8. Boomplaas

This limestone cave site is located in the Cango River valley, north of Oudtshoorn in the Western Cape province. Excavations began in 1974 and have continued since then (Klein 1978), showing stratified deposits and distinct layers. The majority of the faunal remains recovered from the site suffered post-depositional damage and have been reduced to small fragments, and are therefore difficult to identify even to body part. Related to this, there were challenges in separating closely related species and many were thus compounded in processes of categorization (Klein 1978). The existing chronology of the site has been revised using accelerator mass spectrometry (AMS) radiocarbon dating, and despite some inversions of dates across the layers, the dates are said to be reliable (Pargeter *et al.* 2018). The overall occupational age range given for the site is 51 200 (±2600) BP - 11 930 (±50) BP (Pargeter *et al.* 2018). Both *E. capensis* and *E. quagga* are recorded from the site, although *E. quagga* was difficult to separate from other zebra species and was thus placed in a composite category (Klein 1978). Only one *E. capensis* specimen is recorded, and it is unclear which skeletal part this assignment was based on.

9. Nelson Bay Cave

This site is situated on the Robberg Peninsula near Plettenberg Bay, in the Western Cape province. Deep pit excavations were conducted from the 1970s, revealing a long and detailed history of

occupation at the cave (Klein 1972). Excavations have revealed an array of mammalian fossils, with the composition of fauna changing significantly through time to reveal changing climates as well as disappearances of species towards the terminal Pleistocene. The site was initially poorly dated due to mixtures of samples and broad errors in $^{14}C$ dates obtained (Loftus *et al.* 2016). However, the sequence within the cave has been considered as secure, and new radiocarbon dates have placed the site at 23 355 - 5730 BP (Loftus *et al.* 2016). It has, nevertheless, been noted that there are problems of clarity in terms of the exact timing between layer transitions and that refining is necessary.

10. Byneskranskop

This cave site is located at the coastal plain junction (which is relatively flat) and foothills of the southern Cape Folded Mountains. The first test pit at the site was dug in 1973 indicating a long occupational sequence in the area (Schweitzer and Wilson 1978). The faunal remains recovered from the site altered throughout the sequence, particularly with an increase in shellfish, seal and fish in the younger layers (Klein and Cruz-Uribe 1983). At the same time as changes in marine animals were occurring, mammalian fauna changed too; from an abundance of grazers such as zebra, to more browsers such as grysbok (Klein and Cruz-Uribe 1983). It is known that the upper layers of the cave were disturbed by prior unlawful digging, and parts of the deposits were thrown towards the front of the cave and consequently shifted down the talus slope (Schweitzer and Wilson 1978). Moreover, the stratigraphy of the deposit is not clearly differentiated, and only after material was recovered from defined units based on features such as hearths, were researchers able to place them into 19 named ‘layers’ (Schweitzer and Wilson 1978). The site was redated using

AMS $^{14}C$, and although there are inversions of dates indicating possible mixing, the range has been given as 17 105 - 1870 BP (Loftus *et al.* 2016).

11. Florisbad

This is an open-air spring site, located northwest of Bloemfontein in the Free State province. Materials from the site were first collected in 1917, and about two decades later a number of spring vent deposits were opened up, revealing various types of fossils (Kuman *et al.* 1999). Once excavations began it was determined that there are seven meters of complex stratigraphy (Kuman and Clarke 1986). Dating of these layers was attempted, often with problematic or conflicting results (Kuman *et al.* 1999). The Florisbad faunas from the later Middle Pleistocene and the Upper Pleistocene serve as the type assemblage for MSA fauna in southern Africa, yet are poorly dated (Kuman and Clarke 1986). The Holocene deposits are the only sequences that have been successfully dated (Kuman and Clarke 1986). A tooth sample from the well-known hominin fossil found at the site was directly dated via electron spin resonance (ESR), obtaining an age of 259 000 +- 35 000 years old (Grün *et al*. 1996). Optically stimulated luminescence (OSL) dating was applied to sediment samples, which gave an age range from 279+-47 ka to 146+-15 ka. Although saturation problems cause larger errors, these results confirm the large age-span for the site (Grün *et al*. 1996). Test pit sediments gave a spread of ESR dates, likely due to material being reworked as a result of spring action (Grün *et al.* 1996). Using these two techniques in conjunction, the MSA occupational sequence is thought to date roughly from 300 - 100 ka (Grün *et al.* 1996, Ecker and Lee-Thorp 2018).

12. Calvinia

Calvinia is a regional town in the Northern Cape province, just south of the Hantam mountains. While much has been documented on the history of the town – its founding, its place in the Anglo Boer War, its architecture (Amschwand 2019) – virtually nothing of its archaeological history has been reported. There is no excavation history, as well as no account of how the equid material from here were recovered. In addition to no context, no dates have been assigned to the material.

13. Mahemspan

The site is situated on a farm and lies between the localities of Hoopstad and Wesselsbron in the Free State province. Initial excavations took place in the 1930s and 1940s, and were followed up again in 1994 (Brink 2005, Brink *et al.* 2015). The site is now part of a ploughed land, covered by aeolian sand and has not revealed any new *in situ* fossil material (Brink *et al.* 2015). Many of the fossils from the site are fairly complete, and much of it is surrounded by calcium carbonate deposits which infer a marsh-like palaeoenvironment at the time of deposition (Brink 2005). The pattern of taxonomy at the site is viewed as representing a period of intense aridification (Brink 2005). Based on the nature of the large faunal collection present, many broad ages have been posited by various researchers. Dental specimens from ungulates and their attached carbonates were submitted for ESR analysis and revealed a date of 12 ka and 13-17 ka (Brink 2005, Ecker and Lee-Thorp 2018).

14. Cave of Hearths/Makapansgat

This well-known rock shelter is found high up on the left of the Makapan Valley in the Northern province. After the site's initial discovery, only intermittent excavation of fossils from collapsed breccia took place for a decade, and systematic excavations only began in 1947 (Tobias 1971). Stratigraphy of the site is said to be relatively clear apart from an area where slumps have occurred

into a ‘swallow hole’ (Latham and Herries 2004). The majority of the fossil bone and teeth recovered from the site come from mixed deposits, making it difficult to separate materials or clearly distinguish taxonomies (Klein 1988). $C^{14}$ dates from the site suggested that the MSA layers formed during the very late Pleistocene, between 17 ka and 11 ka BP, however these dates were not in stratigraphic order (Klein 1988). These ages were later regarded as too young, likely as a result of contamination of samples. Equid teeth are found in abundance, and have all been assigned to either *E. capensis* or *E. quagga* based on size (Churcher 2000). Similarly to Elands Bay Cave, many specimens have been assigned as ‘*E. capensis/quagga*’ as they were intermediate in appearance and difficult to identify. The broader Makapansgat Formation is a significant complex for having revealed at least 35 hominin fossils, and has been dated via palaeomagnetism obtaining an age range of 2.9 Ma to 3.32 Ma (McFadden *et al.* 1979).

15. Kalkbank

This farm site lies northwest of Polokwane in the Limpopo province (Mason *et al.* 1958). Excavations began by removing the limestone cover of the site with dynamite, exposing various fragments of bones, teeth and artefacts. Kalkbank is rare in that its representation of animal bones are preserved in conjunction with what are assumed to be MSA tools at an open-air site (Hutson and Cain 2008), and the remains are all only found in high concentration areas. Identification of faunal specimens proved difficult due to their fragmentary nature, and typically only genera could be concretely determined (Hutson and Cain 2008). Acquiring reliable dates has proved difficult with Kalkbank as is the case in most open-air localities, and relative dating together with $^{14}C$ calcrete samples have been used previously in attempts to determine the site’s chronology (Hutson 2006). The deposit has been compared to that of Cave of Hearths due to its proximity (it is in fact

roughly 110km from the site), and hence has been assigned an approximate age based on this (Hutson and Cain 2008). Calcrete is known to recalcify through seasonal changes, and this as well as it not being directly associated with the fossils, make the attained $^{14}C$ dates subject to debate (Hutson 2006, Hutson and Cain 2008). The minimum $^{14}C$ date for the site was 17 000 BP, obtained from the lowest calcrete hardpan. However, researchers have favoured dating the site from stone tool types and associated fauna due to possible carbon contamination (Mason 1958). Due to the nature of the tools recovered, the site has been associated with the MSA, and the recovered fauna could be from as far back as 500 ka all the way to the Pleistocene/Holocene boundary (Hutson 2006, Hutson and Cain 2008).

16. Swartkrans

This is one of several cave sites in the Sterkfontein Valley in Gauteng province, and is one of the most well renowned due to the wealth of *Homo* and *Paranthropus* remains ascribed to it (Brain 1993, Balter *et al.* 2008). Exploration at Swartkrans began in the 1940s, and it has been noted that the stratigraphy of the site is incredibly complex and that stages of deposition have been generalized (Brain 1993, de Ruiter 2003). Over time the cave was filled with calcified breccias, which resulted in a complex buildup of sediments that are challenging to date (Balter *et al.* 2008). Radiocarbon dates have placed the youngest layer at under 11 ka, and ESR dates placed the oldest at 1.6 Ma (de Ruiter 2003). It is important to note that ESR dating has been employed at the site in a variety of different studies and has continued to produce wide and variable results – the same is the case for dating via cosmogenic nuclide burials (Gibbon *et al*. 2014). While ESR may allow for precise dating of the fossils, researchers are still reliant on the fauna to estimate ranges due to a lack of other cross checking techniques (de Ruiter 2003). U-Pb methods were applied to bovid

enamel at the site and gave a maximum age of 1.83 ± 1.38 Ma (Balter *et al.* 2008). Upon close examination of the fauna recovered at the site, it has been presumed that Members 2 and 3 of the formation are contemporaneous; however, geochronological evidence points to the reworking of these deposits. Hence, as in most southern African palaeontological sites, discussions of correlation between fauna and the first/last appearances of species can only be done with great caution (de Ruiter 2003).

17. Plovers Lake

This is a dolomitic cave site located in the Bloubank Valley in Gauteng province, and since excavations began, has revealed a diversity of faunal, human and stone tool material (de Ruiter *et al*. 2008). Since its exposure, the fossiliferous breccia has continued to be investigated since the 1980s, and it has been noted that upon removal of the breccia there is the absence of clear stratigraphy (Thackeray and Watson 1994). The site consists of a disturbed, *ex situ* unit above what appears to be a relatively undisturbed *in situ* unit, both of which consist of similarly composed fauna (taxonomically, taphonomically and ecologically) (de Ruiter *et al.* 2008). Two flowstone layers frame the *in situ* deposition, and uranium-series (U-series) dates for the capping and underlying flowstones present as 62.9 (±1.3) ka and 88.7 (±1.6) ka respectively (de Ruiter *et al*. 2008).

18. Gladysvale

This site is situated in the Krugersdorp District, just northeast of Sterkfontein in Gauteng province. It is a cave system that consists of a series of fossiliferous deposits (Lacruz *et al.* 2003) that have been excavated since the 1990s. Gladysvale also comprises open-air deposits that have been

exposed as a result of the cave roof's collapse (Lacruz *et al.* 2003). The site consists of decalcified external deposits, of which the sediments do not show clear stratigraphy; and calcified breccias that are horizontally stratified (Lacruz *et al*. 2002, Lacruz *et al.* 2003). It has been noted that there was likely movement of fossils within the decalcified deposits, thus taking them out of context and chronology (Lacruz *et al.* 2003). ESR dating performed on three fossil bovid teeth at the site provided a broad range of 578 ka - 830 ka for the deposit (Lacruz *et al.* 2002, Lacruz *et al.* 2003); dates that have been questioned due to the unknown uranium uptake of these teeth (Pickering *et al.* 2007). U-series dates performed on numerous flowstone deposits, however, have provided a much longer depositional range of 570 ka – 7 ka (Pickering *et al.* 2007), though the dated flowstones do not show any correlative pattern in the timing of their formation with glacial cycles.

19. Sand River

This is a large drainage system that runs through the central Free State province. The materials were collected during investigations of the erosional surfaces (Brink *et al*. 1999), but unfortunately very few publications exist on the recovered fossils from the area. All fossils are derived from erosional dongas along the Sand River drainage system, though no systematic excavations have taken place along this drainage. Exact locality of the equid material included in this research (identified only to genera) are unknown (pers. comm. Lloyd Rossouw). No direct dates have been obtained for the recovered material, but based on morphological and species comparisons an approximated age of 400 ka – 100 ka has been postulated (Brink *et al.* 1999).

# Appendix B

## Linear Length and Breadth Measurements (LM)

| Catalogue Number | Length (mm) | Breadth (mm) |
|---|---|---|
| CAR3 C6 K8-1 2 | 32.44 | 21.79 |
| CAR3 C6 K8-1 3 | 30.39 | 22.77 |
| GBAN F5 | 33.23 | 21.46 |
| CL3 BGM P15/12 | 30.8 | 18.74 |
| CL3 015 | 32 | 14.72 |
| CL3 BP Q15 | 33.14 | 20.54 |
| Q34A | 30.3 | 20.56 |
| 6634 | 28.31 | 20.75 |
| 209705 | 29.55 | 18.71 |
| 209700 | 33.32 | 20.45 |
| 2206 | 30.99 | 20.6 |
| 3899-C | 30.11 | 17.19 |
| 1894 | 28.58 | 15.22 |
| 1970 | 32.5 | 24.15 |
| 10068F | 27 | 17.22 |
| 10068B | 26.81 | 18.61 |
| 10068C | 30.72 | 17.88 |
| 10068A | 31.4 | 20.19 |
| 20971A | 32.74 | 24.5 |
| 17562 | 28.09 | 19.14 |
| 11414 | 31.76 | 19.73 |
| GV5350 | 32.64 | 18.52 |
| GVL1-115-B1 | 28.45 | 18.63 |
| GV7961 | 38.24 | 18.76 |
| GV4523 | 30.8 | 18.52 |
| GVD1-104-B24 | 34.41 | 22.83 |
| 42258 | 34.82 | 20.39 |
| 31932 | 33.43 | 19.28 |
| 19616 | 30.55 | 17.69 |
| 36437 | 38.3 | 18.63 |
| COH650 | 32.13 | 21.87 |
| COH440 | 37.8 | 19.68 |
| KB594 | 30.66 | 21.76 |
| KB595 | 31.72 | 18.31 |
| COH553 | 34.16 | 22.5 |
| COH24-25 | 29.65 | 18.49 |
| COH415 | 30.43 | 22.16 |

| | | |
|---|---|---|
| COH550 | 37.56 | 20.24 |
| COH495 | 28.84 | 17.81 |
| COH497 | 35.37 | 20.52 |
| P28 19A | 33.47 | 22.12 |
| COH404 | 27.97 | 19.5 |
| PKA210 | 31.3 | 17.59 |
| COH557 | 29.94 | 20.73 |
| COH442 | 30.38 | 17.17 |
| KAR12-219 | 29.6 | 16.7 |
| KAR12-140 | 28 | 15.5 |
| KAR12-271 | 27.2 | 14.7 |
| KNM-AB 24228 | 27.9 | 15.7 |
| FLO2501 C1479 | 22.65 | 15.67 |
| FLO4866 | 20.34 | 12.55 |
| FLO6013 C2921 | 23.28 | 12.28 |
| FLO6006 C1522 | 22.81 | 13.2 |
| FLO6004 C2921 | 21.68 | 13.08 |
| FLO6051 SAM10622 | 25.03 | 14.62 |
| FLO2568 | 23.84 | 14.51 |
| FLO6001 C1522 | 25.73 | 11.79 |
| FLO4635 C1522 | 23.4 | 13.74 |
| FLO4608 C1522 | 21.85 | 12.36 |
| FLO2609 | 21.46 | 14.33 |
| FLO2562 C1484 | 24.11 | 11.28 |
| FLO2571 C1484 | 24.46 | 12.95 |
| FLO6055 SAM10622 | 28.09 | 14.52 |
| FLO6052 SAM10622 | 23.54 | 13.04 |
| FLO2579 | 25.04 | 11.54 |
| PV12004 | 22.6 | 14.34 |
| KB618 | 25.83 | 17.97 |
| 379 | 24.63 | 17.03 |
| 371 | 26.47 | 15.3 |
| 376 | 26.88 | 17.01 |
| 372 | 24.25 | 16.7 |
| 377 | 24.65 | 16.79 |
| COH Tu/15-19/28-30 | 26.93 | 20.2 |
| COH Tu/15-19 | 27.39 | 16.39 |
| COH28-30 | 26.7 | 18.4 |
| COH548 | 27.4 | 13.17 |
| COH590 | 29.5 | 15.44 |
| COH582 | 23.34 | 16.8 |
| COH472 | 27.47 | 16.33 |
| CL1L | 34.17 | 15.81 |

| | | |
|---|---|---|
| CL2 P12 | 30.53 | 14.61 |
| CL1 N15 | 27.4 | 19.63 |
| BPL4 016 | 30.02 | 15.98 |
| CAR3 C6 K8-1 1 | 31.63 | 31.21 |
| CL4 BBG | 30.39 | 23.3 |
| CL3 P14 | 34.15 | 26.53 |
| CL3 BGMOU P14 | 29.13 | 31.22 |
| CL3 BG Q14 | 25.55 | 26.39 |
| WCRP 2110 | 34.46 | 34.54 |
| WCRP 2049 | 37.4 | 33.11 |
| WCRP 2385 | 33.33 | 31.16 |
| WCRP 2102 | 30.11 | 31.01 |
| WCRP 2100 | 28.57 | 32.35 |
| WCRP 9387 | 29.39 | 30.38 |
| WCRP 9389 | 27.39 | 30.97 |
| N/A | 36.91 | 33.73 |
| 2105 | 32.09 | 26.5 |
| EQ18 2500A | 30.2 | 30.71 |
| EQ8 2501C | 31.7 | 31.08 |
| 2505B | 37.12 | 33.92 |
| 2505A | 32.6 | 32.11 |
| 9146A | 29.21 | 28.75 |
| 16799 | 31.94 | 31.6 |
| 2810 | 30.06 | 29.25 |
| 1895 | 33.74 | 32.81 |
| TEX2619-I | 29.97 | 32.1 |
| TEX2619-I-I | 28.52 | 30.13 |
| TEX2619-B | 30.53 | 31.93 |
| TEX2619-G | 33.86 | 34.66 |
| TEX2619-C | 33.73 | 32.74 |
| 2499A | 41.65 | 34.44 |
| 2499B | 36.1 | 33.93 |
| 2499C | 31.86 | 32.55 |
| 2499D | 31.44 | 31.08 |
| GV7598 | 26.18 | 27.59 |
| GVD1-220 | 36.16 | 29.41 |
| GV391-B133 | 31.95 | 27.32 |
| GV402 | 29.2 | 24.11 |
| 28881 | 39.3 | 26.77 |
| COH160 | 33.53 | 30.95 |
| COH127 | 29.9 | 26.97 |
| COH167 | 28.56 | 29.39 |
| COH69 | 31.19 | 30.12 |

| | | |
|---|---|---|
| COH163 | 29.3 | 28.41 |
| KB566 | 30.73 | 32.44 |
| KB561 | 41.95 | 38.12 |
| KB583 | 33.12 | 33.46 |
| KB580 | 31.83 | 32.59 |
| KB45 | 33.78 | 37.87 |
| KB579 | 30.6 | 36.79 |
| KB581 | 34.12 | 34.05 |
| KB1565 | 41.81 | 38.87 |
| KB567 | 36.07 | 38.82 |
| KB45 | 38.08 | 34.51 |
| KB572 | 29.41 | 35.08 |
| CD5881 | 31.9 | 31.37 |
| CD9293 | 36.84 | 26.24 |
| 390 | 38.91 | 27.68 |
| COH10 | 32.65 | 34.94 |
| COH53 | 42.25 | 31.44 |
| COH59 | 32.45 | 31.77 |
| PKA218 | 29.2 | 34.02 |
| PKA216 | 30.16 | 31.4 |
| PKA211 | 30.07 | 31.61 |
| PKA222 | 31.92 | 29.61 |
| PKA213 | 31.27 | 34.43 |
| PKA217 | 36.36 | 30.1 |
| PKA220 | 28.85 | 33.94 |
| PKA221 | 35.69 | 31.21 |
| 392 | 30.88 | 32.76 |
| 5016 | 32.2 | 30.4 |
| 1019 | 29.2 | 29 |
| 4939 | 28.2 | 27.8 |
| COH68 | 27.24 | 27.73 |
| COH170 | 26.22 | 26.34 |
| COH161 | 27.14 | 27.83 |
| COH276 | 25.57 | 24.81 |
| COH227 | 23.7 | 27.42 |
| COH169 | 28.92 | 28.68 |
| COH360 | 25.51 | 27.22 |
| COH164 | 28.26 | 26.69 |
| COH188 | 26.18 | 26.38 |
| COH136 | 32.16 | 30.82 |
| COH28 | 32.17 | 34.9 |
| COH155 | 29.19 | 28.83 |
| N/A | 26.63 | 27.81 |

| | | |
|---|---|---|
| COH3 | 27.84 | 28.45 |
| COH134 | 26.34 | 22.66 |
| COH173 | 25.66 | 25.78 |
| COH370 | 30.72 | 22.44 |
| BP/4/147 | 27.34 | 28.98 |
| BP/4/911 | 25.59 | 25.16 |
| PL5854 | 27.59 | 27.09 |
| PL17743 | 25.14 | 23.95 |
| PV17790 | 21.35 | 23.7 |
| 13/198 | 26.75 | 24.68 |
| 323 | 28.53 | 25.88 |
| 130 | 23.04 | 26.59 |
| KB653 | 24.37 | 25.18 |
| KB704 | 28.15 | 26 |
| KB676 | 26.96 | 26.53 |
| KB702 | 23.54 | 24.8 |
| KB680 | 23.96 | 25.23 |
| KB677 | 27.23 | 27.78 |
| KB685 | 26.98 | 24.69 |
| KB700 | 25.3 | 24.94 |
| KB654 | 27.6 | 27.53 |
| KB691 | 24.57 | 26.06 |
| KB655 | 26.93 | 28.03 |
| KB705 | 22.26 | 24 |
| KB659 | 28.95 | 27.2 |
| KB692 | 23.44 | 23.88 |
| KB695 | 26.91 | 25.72 |
| KB679 | 22.69 | 23.37 |
| KB672 | 28.1 | 22.46 |
| 328 | 26.05 | 25.67 |
| 359 | 21.27 | 26.77 |
| COH21-24 | 24.95 | 27.09 |
| COH15-19 | 22 | 24.68 |
| COH27 | 23.85 | 26.46 |
| COH54 | 28.13 | 27.59 |
| COH5 | 29.45 | 27.53 |
| COH18 | 26.64 | 27.62 |
| COH44 | 24.57 | 24.97 |
| 19HO | 23.19 | 25.11 |
| COH245 | 25.14 | 26.8 |
| COH165 | 26.31 | 22.73 |
| COH111 | 29.81 | 24.15 |
| COH130 | 26.63 | 23.22 |

| | | |
|---|---|---|
| COH141 | 26.66 | 26.67 |
| COH594 | 36.57 | 17.33 |
| SAM-AA B6 YSL | 23.84 | 27.12 |
| SAM-AA D4 YSL | 28.96 | 24.82 |
| 14/38 | 29.49 | 29.44 |
| 15/16 | 24.33 | 28.27 |
| 14/35 | 22.74 | 24.76 |
| 14/37 | 24.28 | 29.02 |
| 14/36 | 23.93 | 29.33 |
| 13/02 | 29.18 | 27.92 |
| CL1 | 24.21 | 16.01 |
| KNM-AB 24280 | 27.4 | 26.2 |
| 11/19 | 26.64 | 23.66 |
| BP/4/149 | 21.74 | 24.3 |
| KNM-OG 22833 | 25.8 | 27.2 |

# Appendix C

## Geometric Morphometric Centroid Size and PC Scores

| Catalogue Number | Centroid Size | PC1 | PC2 | PC3 | PC4 | PC5 |
|---|---|---|---|---|---|---|
| SR4-9 (0001) | 14.2679 | 0.0510 | -0.0738 | 0.0142 | -0.0238 | 0.0022 |
| SR41 (0002) | 12.8099 | -0.0879 | 0.0079 | 0.0244 | 0.0003 | -0.0128 |
| VLA130 C1522 | 12.2847 | -0.0655 | -0.0532 | -0.0352 | 0.0261 | 0.0352 |
| VLA85 C1522 | 10.4412 | -0.0728 | -0.0105 | -0.0087 | 0.0065 | 0.0280 |
| VLA77 C1522 | 9.7841 | 0.0709 | -0.0208 | 0.0174 | 0.0069 | 0.0040 |
| VLA72 C1522 | 10.6691 | 0.0864 | -0.0180 | 0.0182 | -0.0247 | -0.0130 |
| VLA28 C1522 | 11.4737 | -0.0336 | -0.0122 | 0.0153 | -0.0006 | 0.0037 |
| VLA19 C1522 | 10.9845 | 0.0758 | 0.0089 | 0.0131 | 0.0498 | 0.0040 |
| VLA75 FLO4873 | 8.5711 | 0.0231 | 0.0273 | 0.0211 | 0.0261 | 0.0261 |
| FLO2501 C1479 | 9.8990 | 0.0636 | 0.0437 | 0.0238 | 0.0074 | -0.0050 |
| FLO6006 C1522 | 9.1798 | 0.0514 | 0.0039 | -0.0164 | 0.0134 | 0.0083 |
| FLO2568 | 10.1788 | 0.0862 | -0.0723 | 0.0040 | 0.0158 | -0.0189 |
| FLO4635 C1522 | 9.7018 | 0.0865 | -0.0341 | 0.0296 | 0.0079 | 0.0107 |
| FLO4608 C1522 | 8.9789 | 0.0644 | 0.0114 | 0.0178 | 0.0097 | 0.0042 |
| FLO6051 SAM10622 | 10.7125 | -0.0736 | -0.0692 | 0.0293 | 0.0034 | 0.0630 |
| FLO6004 C2921 | 9.2099 | 0.0453 | 0.0205 | 0.0148 | 0.0179 | 0.0094 |
| FLO2609 | 11.7724 | -0.0882 | -0.0009 | 0.0220 | 0.0272 | 0.0015 |
| FLO2562 C1484 | 9.6409 | 0.0671 | -0.1007 | -0.0369 | 0.0028 | 0.0447 |
| FLO6055 SAM10622 | 11.1998 | -0.0570 | -0.0801 | 0.0321 | -0.0091 | -0.0010 |
| FLO6052 SAM10622 | 9.8424 | 0.0613 | 0.0122 | 0.0266 | 0.0288 | 0.0006 |
| FLO2579 | 9.3924 | 0.0724 | -0.1008 | -0.0230 | -0.0159 | 0.0230 |
| FLO6027 C1582 | 9.6473 | 0.0664 | -0.0041 | 0.0220 | 0.0229 | 0.0135 |
| FLO6023 C1522 | 12.3517 | 0.1194 | -0.0954 | -0.0015 | -0.0101 | -0.0030 |
| FLO6024 | 10.6980 | 0.0581 | -0.0176 | 0.0231 | 0.0239 | 0.0020 |
| FLO2545 C2609 | 11.2313 | 0.0747 | -0.1131 | -0.0142 | 0.0016 | -0.0004 |
| FLO4617 C1522 | 9.2467 | 0.0706 | 0.0443 | 0.0305 | 0.0314 | -0.0179 |
| FLO2700 C1522 | 9.1646 | 0.0361 | 0.0834 | 0.0194 | -0.0113 | 0.0256 |
| FLO6030 | 9.5130 | 0.0553 | 0.0246 | 0.0155 | 0.0566 | 0.0077 |
| FLO6029 C1484 | 10.9867 | 0.0628 | -0.0293 | 0.0287 | 0.0339 | 0.0002 |
| FLO6053 SAM10622 | 9.4396 | 0.0318 | -0.0068 | 0.0329 | -0.0033 | 0.0458 |
| FLO6025 C1522 | 10.2085 | 0.0148 | 0.0172 | 0.0319 | 0.0069 | 0.0133 |
| FLO6026 C1522 | 10.0699 | 0.0167 | 0.0244 | 0.0337 | 0.0012 | -0.0012 |
| FLO6033 C1522 | 11.3480 | -0.1134 | -0.0830 | 0.0281 | 0.0697 | -0.0267 |
| FLO2583 C2602 | 11.8793 | -0.1308 | -0.0418 | 0.0528 | -0.0096 | 0.0540 |

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|---|---|---|---|---|---|---|
| FLO6028 | 11.3771 | -0.0912 | -0.0649 | 0.0136 | 0.0237 | 0.0338 |
| FLO6014 C1522 | 10.6766 | -0.0490 | -0.0743 | 0.0139 | -0.0003 | 0.0528 |
| FLO6034 C1522 | 12.2830 | -0.0899 | 0.0064 | 0.0087 | 0.0130 | -0.0114 |
| FLO6038 C1522 | 11.7343 | -0.0814 | 0.0175 | 0.0041 | -0.0098 | 0.0132 |
| FLO6009 C1522 | 10.4930 | -0.0721 | 0.0284 | 0.0166 | 0.0141 | 0.0029 |
| FLO6035 C1522 | 10.7521 | -0.0969 | 0.0162 | 0.0309 | 0.0160 | -0.0134 |
| FLO6045 C1522 | 11.4090 | -0.0559 | 0.0175 | 0.0089 | -0.0020 | 0.0038 |
| FLO6011 C1522 | 11.4438 | -0.0391 | 0.0194 | 0.0210 | 0.0499 | 0.0219 |
| FLO6010 C1522 | 11.4945 | -0.0551 | -0.0182 | 0.0039 | 0.0406 | 0.0058 |
| PK A210 | 13.0118 | 0.0560 | -0.0073 | 0.0276 | -0.0004 | 0.0196 |
| EC1008 | 10.9535 | 0.0769 | -0.0013 | 0.0310 | 0.0017 | 0.0192 |
| 23K 1232 | 10.2844 | 0.0626 | -0.0160 | 0.0109 | -0.0121 | -0.0173 |
| 23K 1425 | 10.4070 | 0.0690 | -0.0268 | 0.0095 | -0.0183 | -0.0230 |
| 22J 1210 | 9.9214 | 0.0614 | -0.0728 | 0.0355 | 0.0155 | -0.0042 |
| EC499 | 11.5189 | 0.0512 | -0.0489 | 0.0133 | 0.0111 | -0.0090 |
| EC378 | 9.8239 | 0.0108 | -0.0080 | 0.0192 | 0.0446 | 0.0111 |
| EC1274 | 10.0958 | 0.0646 | 0.0222 | -0.0119 | 0.0091 | -0.0086 |
| EC500 | 9.7941 | 0.0411 | 0.0056 | 0.0131 | 0.0239 | 0.0027 |
| EC1173 | 10.0936 | 0.0609 | 0.0223 | 0.0248 | 0.0320 | 0.0219 |
| EC1186 | 10.1586 | 0.0813 | 0.0039 | 0.0120 | -0.0122 | -0.0078 |
| EC934 | 11.2298 | 0.0472 | 0.0376 | 0.0117 | 0.0065 | -0.0010 |
| EC1071 | 10.2400 | 0.0273 | -0.0005 | 0.0212 | 0.0629 | -0.0006 |
| EC1275 | 11.2659 | 0.0472 | 0.0063 | 0.0130 | 0.0246 | 0.0080 |
| EC959 | 10.4990 | 0.0275 | 0.0450 | 0.0434 | 0.0629 | 0.0095 |
| EC1283 | 12.0669 | 0.0929 | -0.0261 | -0.0081 | -0.0075 | -0.0191 |
| EC1208 | 9.9137 | 0.0365 | 0.0025 | 0.0178 | 0.0515 | 0.0061 |
| EC216 | 13.4005 | -0.1140 | 0.0110 | 0.0284 | -0.0592 | 0.0576 |
| EC1069 | 12.0762 | -0.0354 | -0.0018 | 0.0190 | -0.0006 | 0.0288 |
| EC971 | 10.8256 | -0.0904 | 0.0197 | 0.0368 | 0.0382 | -0.0065 |
| EC1021 | 12.6267 | -0.0594 | 0.0133 | -0.0050 | -0.0143 | 0.0030 |
| EC1278 | 11.2316 | -0.0869 | 0.0030 | 0.0233 | 0.0014 | 0.0036 |
| EC1025 | 11.1098 | -0.0733 | 0.0292 | 0.0152 | 0.0121 | 0.0172 |
| EC2 | 10.6704 | -0.0624 | -0.0030 | 0.0114 | 0.0446 | 0.0149 |
| EC1022 | 11.3970 | -0.0805 | 0.0112 | -0.0177 | 0.0391 | -0.0185 |
| EC1016 | 11.4592 | 0.0003 | 0.0510 | 0.0296 | 0.0191 | 0.0138 |
| EC1168 | 11.5171 | -0.0785 | 0.0067 | 0.0158 | 0.0267 | -0.0091 |
| EC396 | 12.5528 | -0.0881 | -0.0010 | 0.0053 | 0.0173 | 0.0063 |
| EC400 | 12.2856 | -0.0468 | 0.0446 | 0.0133 | -0.0128 | 0.0285 |
| EC1281 | 11.6530 | -0.1062 | 0.0138 | -0.0022 | 0.0123 | 0.0197 |
| EC1199 | 11.8984 | -0.0542 | -0.0104 | 0.0138 | 0.0057 | 0.0178 |
| EC1017 | 11.4878 | -0.0563 | 0.0115 | 0.0331 | 0.0145 | -0.0249 |
| EC1098 | 10.9750 | -0.0241 | -0.0280 | 0.0221 | 0.0134 | -0.0048 |
| J19 8 | 11.5183 | 0.0414 | -0.1216 | 0.0026 | 0.0103 | -0.0148 |

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|---|---|---|---|---|---|---|
| EC1055 | 12.4453 | -0.0866 | -0.0247 | -0.0119 | 0.0121 | -0.0447 |
| C.2123 | 9.9322 | 0.0449 | -0.0751 | -0.0069 | 0.0571 | -0.0028 |
| C1775 | 12.0344 | -0.0833 | -0.0134 | 0.0296 | 0.0286 | -0.0253 |
| C2121 | 11.3809 | -0.0292 | -0.0351 | -0.0059 | 0.0221 | 0.0138 |
| C1973 | 12.5490 | 0.0862 | -0.0270 | 0.1054 | -0.0461 | -0.0105 |
| C2119 | 14.6978 | -0.0648 | 0.0232 | 0.0165 | 0.0321 | -0.0135 |
| COH550 | 13.4146 | 0.1087 | -0.0471 | 0.0083 | -0.0245 | -0.0106 |
| COH415 | 12.7298 | 0.0572 | -0.0163 | 0.0440 | 0.0340 | 0.0157 |
| COH2425 | 12.4713 | 0.0738 | 0.0287 | 0.0473 | 0.0244 | 0.0146 |
| COH28 - 30 | 11.9476 | -0.0586 | 0.0492 | -0.0012 | -0.0090 | 0.0032 |
| COH582 | 10.5191 | 0.0275 | 0.0259 | 0.0167 | 0.0370 | -0.0134 |
| COH Tu - 15 - 19 | 10.6284 | 0.0430 | -0.0161 | 0.0381 | 0.0235 | 0.0141 |
| COH495 | 12.3824 | -0.0549 | 0.0214 | 0.0267 | -0.0391 | 0.0188 |
| COH404 | 12.7192 | 0.0437 | 0.0200 | 0.0066 | 0.0066 | 0.0339 |
| COH442 | 12.2502 | -0.0611 | -0.1163 | 0.0537 | 0.0000 | -0.0134 |
| 377 | 10.1867 | 0.0439 | -0.0237 | 0.0105 | 0.0409 | 0.0220 |
| 372 | 10.0139 | 0.0586 | -0.0173 | 0.0182 | 0.0707 | 0.0083 |
| 376 | 12.0579 | -0.0536 | -0.0458 | 0.0525 | -0.0049 | -0.0061 |
| KB595 | 12.7818 | -0.0336 | -0.0297 | 0.0088 | 0.0035 | 0.0432 |
| KB618 | 9.8705 | 0.0644 | -0.0009 | 0.0285 | 0.0247 | 0.0147 |
| 42258 | 14.1995 | -0.0547 | -0.0607 | 0.0110 | -0.0256 | -0.0093 |
| Pv12004 | 9.3551 | 0.0225 | 0.0018 | 0.0240 | -0.0041 | 0.0130 |
| GV7961 | 14.7466 | 0.0695 | -0.0236 | -0.0245 | -0.0585 | -0.0136 |
| COH472 | 10.8407 | 0.0645 | 0.0108 | 0.0188 | -0.0560 | 0.0008 |
| COH594 | 11.3809 | -0.0403 | 0.0449 | -0.0022 | -0.0005 | 0.0093 |
| BP/4/152 | 12.6788 | -0.0737 | 0.0002 | 0.0113 | 0.0033 | -0.0147 |
| BP/4/147 | 11.6325 | -0.1168 | -0.0235 | 0.0655 | 0.0479 | -0.0211 |
| BP/4/911 | 11.1744 | 0.0276 | 0.0221 | 0.0225 | 0.0608 | -0.0408 |
| BP/4/929 | 12.2950 | -0.0380 | 0.0523 | 0.0193 | 0.0398 | -0.0524 |
| Q34A | 12.8685 | 0.0639 | 0.0337 | 0.0610 | -0.0412 | -0.0132 |
| 20970K | 13.9314 | 0.0199 | 0.0730 | 0.0255 | -0.0365 | -0.0244 |
| 2504A | 12.4702 | 0.0544 | 0.0266 | 0.0599 | -0.0454 | -0.0094 |
| 20974C | 13.8427 | -0.0381 | -0.0258 | 0.0046 | -0.0474 | 0.0139 |
| 20974B | 14.9256 | -0.0814 | -0.0250 | 0.0186 | -0.0488 | 0.0454 |
| TEX2625 | 14.1344 | -0.0785 | -0.0281 | 0.0777 | -0.0239 | -0.0127 |
| 2174 | 12.4789 | 0.0531 | 0.0808 | 0.0458 | -0.0449 | 0.0100 |
| N/A | 13.1456 | 0.0739 | -0.1322 | 0.0035 | 0.0009 | 0.0053 |
| 10068 A-D | 11.5589 | 0.0739 | -0.0046 | 0.0517 | -0.0094 | 0.0169 |
| 3899 - C | 11.9686 | 0.0645 | 0.0319 | 0.0296 | -0.0345 | -0.0036 |
| 1894 | 11.4752 | 0.0740 | 0.0033 | 0.0232 | -0.0026 | 0.0293 |
| 20097IB | 11.2435 | 0.0501 | -0.0140 | 0.0412 | 0.0715 | -0.0045 |
| 209705 | 11.5595 | 0.0822 | -0.0074 | 0.0545 | -0.0012 | -0.0399 |
| 2206 | 11.9331 | 0.0727 | 0.0190 | 0.0388 | -0.0206 | 0.0023 |

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|---|---|---|---|---|---|---|
| 1970 | 13.5238 | -0.0157 | 0.0114 | 0.0955 | -0.0043 | -0.0041 |
| 6634 | 12.5279 | 0.0420 | 0.0064 | 0.0455 | 0.0181 | 0.0253 |
| 10601 | 12.5040 | -0.0271 | 0.0242 | 0.0218 | -0.0030 | -0.0382 |
| 10602 | 14.4906 | -0.1064 | -0.0063 | 0.0428 | -0.0007 | -0.0434 |
| 16864 | 14.4846 | -0.0163 | -0.0139 | 0.0171 | 0.0239 | -0.0126 |
| 15829 | 15.3546 | -0.0551 | -0.0163 | 0.0861 | -0.0649 | 0.0019 |
| 2205 | 13.8147 | -0.0336 | -0.0466 | 0.0593 | -0.0070 | -0.0252 |
| 11414 | 14.3871 | -0.1095 | 0.0169 | 0.0130 | 0.0234 | -0.0162 |
| 17562 | 11.0045 | 0.0902 | 0.0610 | 0.0372 | -0.0018 | 0.0323 |
| 13/295 | 12.4570 | -0.1094 | -0.0081 | 0.0352 | -0.0645 | -0.0107 |
| 13/198 | 11.1973 | 0.0210 | -0.0659 | 0.0222 | -0.0038 | -0.0091 |
| 14/35 | 12.0732 | -0.1036 | 0.0257 | 0.0160 | -0.0188 | 0.0190 |
| 14/37 | 10.4034 | 0.0490 | 0.0737 | 0.0380 | -0.0028 | 0.0059 |
| 13/02 | 10.8865 | 0.0783 | -0.0305 | 0.0791 | -0.0594 | -0.0092 |
| 14/38 | 11.1439 | -0.0125 | 0.1051 | 0.0501 | 0.0112 | 0.0060 |
| 90/16 | 13.8719 | -0.0443 | 0.0193 | 0.0480 | 0.0067 | -0.0313 |
| 11/19 | 11.6349 | 0.0412 | 0.0154 | 0.0301 | 0.0619 | -0.0224 |
| KNM-AB 24228 | 12.0241 | -0.1444 | -0.0066 | 0.0355 | -0.0399 | -0.0135 |
| KNM-AB 24231 | 7.7745 | 0.0815 | -0.0125 | 0.0136 | -0.0231 | 0.0094 |
| 372 | 14.1911 | -0.0799 | -0.0157 | 0.0410 | -0.0252 | 0.0035 |
| 4940 | 11.7336 | 0.0580 | -0.0212 | 0.0322 | -0.0035 | 0.0005 |
| 5373 | 13.2386 | -0.0657 | -0.0157 | 0.0374 | -0.0181 | 0.0453 |
| CAR3 C6 K8-13 | 13.5517 | 0.0466 | 0.0565 | 0.0286 | 0.0370 | 0.0125 |
| CL1 N15 | 12.2416 | -0.0339 | 0.0241 | 0.0665 | -0.0096 | -0.0378 |
| Unmarked | 10.6818 | 0.0500 | -0.0316 | 0.0826 | -0.0481 | -0.0090 |
| COH590 | 10.4811 | 0.0547 | -0.0828 | 0.0309 | 0.0042 | -0.0072 |
| GBAN F5 | 13.9138 | -0.0362 | -0.0374 | 0.0275 | 0.0295 | 0.0262 |
| KAR12-134 | 9.4329 | 0.0369 | -0.0236 | 0.0377 | 0.0131 | -0.0060 |
| KAR12-140 | 11.2198 | -0.0547 | -0.1463 | -0.0103 | -0.0137 | -0.0612 |
| KAR12-271 | 12.1091 | -0.0455 | -0.0176 | 0.0049 | 0.0198 | -0.0004 |
| KAR12-47 | 11.0543 | -0.1154 | -0.0417 | 0.0038 | -0.0159 | -0.0443 |
| KAR13-110 | 8.9647 | 0.0499 | 0.0593 | 0.0051 | -0.0185 | -0.0040 |
| P28 19A | 15.1253 | -0.0815 | -0.0490 | 0.0284 | 0.0457 | 0.0464 |
| 13/198 | 12.0173 | 0.1090 | -0.0388 | 0.0365 | -0.0428 | 0.0403 |
| 11/20 | 13.1733 | -0.0407 | 0.0514 | -0.0106 | -0.0189 | 0.0035 |
| WCRP 9387 | 14.8216 | -0.0324 | -0.0090 | -0.0212 | -0.0056 | -0.0085 |
| WCRP 9387 | 14.9045 | -0.0119 | -0.0246 | -0.0237 | 0.0074 | -0.0139 |
| WCRP 2102 | 15.3561 | 0.0104 | -0.0294 | -0.0279 | -0.0034 | -0.0460 |
| WCRP 2100 | 15.1863 | -0.0421 | -0.0084 | -0.0096 | 0.0006 | -0.0180 |
| WCRP 2385 | 15.6707 | 0.0142 | -0.0432 | -0.0217 | 0.0086 | -0.0317 |
| WCRP 2110 | 16.4613 | -0.0020 | -0.0047 | 0.0138 | -0.0049 | -0.0673 |
| WCRP 2049 | 16.8847 | 0.0265 | 0.0061 | 0.0458 | 0.0025 | -0.0446 |
| 2499A | 16.3495 | 0.0937 | 0.0224 | 0.0046 | -0.0096 | -0.0144 |

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|---|---|---|---|---|---|---|
| 2499B | 15.5907 | 0.0856 | 0.0381 | -0.0031 | 0.0037 | -0.0151 |
| 2499D | 14.6636 | 0.0359 | -0.0120 | -0.0066 | -0.0115 | -0.0042 |
| 2499C | 15.1031 | -0.0018 | -0.0123 | 0.0040 | -0.0260 | -0.0394 |
| TEX2619-C | 16.2044 | 0.0007 | -0.0091 | -0.0027 | -0.0206 | -0.0251 |
| TEX2619-G | 16.5128 | -0.0114 | 0.0044 | -0.0019 | -0.0371 | -0.0224 |
| TEX2619-B | 14.8916 | -0.0561 | -0.0184 | -0.0306 | -0.0095 | -0.0146 |
| TEX2619-I-I | 14.6844 | -0.0777 | -0.0075 | -0.0033 | -0.0017 | -0.0123 |
| TEX2619-I | 14.8263 | -0.0493 | -0.0082 | -0.0535 | 0.0112 | -0.0155 |
| 2505A | 14.9390 | 0.0025 | -0.0100 | 0.0046 | -0.0258 | -0.0307 |
| 9146A | 14.1634 | 0.0311 | 0.0235 | -0.0348 | -0.0280 | -0.0260 |
| 16799 | 14.3594 | 0.0083 | 0.0249 | -0.0064 | -0.0098 | -0.0284 |
| 2810 | 13.9038 | 0.0344 | -0.0402 | 0.0071 | -0.0241 | 0.0233 |
| 1895 | 15.5310 | 0.0017 | 0.0188 | 0.0255 | 0.0047 | -0.0183 |
| EQ8 2501-C | 15.1539 | -0.0388 | 0.0262 | -0.0020 | -0.0102 | -0.0060 |
| EQ18 2500A | 14.6614 | -0.0265 | 0.0250 | -0.0034 | -0.0174 | 0.0013 |
| 2105 | 14.1609 | 0.0940 | 0.0344 | 0.0006 | -0.0243 | -0.0046 |
| 17257 | 14.8718 | 0.0232 | -0.0660 | -0.0081 | -0.0290 | -0.0063 |
| N/A | 16.0399 | 0.0063 | -0.0669 | 0.0359 | -0.0244 | -0.0346 |
| 16660E | 15.0349 | -0.0237 | -0.0265 | -0.0002 | -0.0278 | 0.0106 |
| 16661E | 15.4937 | 0.0049 | -0.0172 | -0.0312 | -0.0326 | 0.0211 |
| 16660C | 16.2694 | 0.0275 | 0.0150 | 0.0049 | -0.0212 | -0.0071 |
| EQ28 2472 | 15.9708 | 0.0378 | 0.0068 | 0.0226 | -0.0222 | -0.0077 |
| 16772 (46) | 16.1444 | -0.0579 | -0.0338 | -0.0046 | 0.0140 | 0.0004 |
| EQ2466 | 15.1548 | -0.0047 | 0.0085 | -0.0142 | 0.0064 | -0.0136 |
| 2590 | 13.5327 | 0.0274 | 0.0170 | -0.0258 | -0.0288 | 0.0025 |
| EQ48 2498B | 15.1327 | -0.0153 | 0.0113 | -0.0226 | -0.0215 | -0.0146 |
| EQ52 2490 | 15.8734 | -0.0180 | 0.0242 | 0.0397 | -0.0233 | -0.0149 |
| 6726 | 15.1684 | -0.0239 | -0.0067 | -0.0033 | -0.0157 | 0.0063 |
| EQ2456 | 15.2847 | 0.0328 | -0.0151 | -0.0007 | -0.0419 | 0.0022 |
| EQ51 2498E | 14.3271 | -0.0273 | 0.0026 | 0.0100 | -0.0200 | 0.0074 |
| EQ31 2474 | 14.4093 | 0.0031 | 0.0163 | -0.0144 | -0.0195 | -0.0040 |
| 5352-E | 15.3951 | -0.0597 | -0.0206 | -0.0023 | -0.0163 | -0.0122 |
| 20798 | 14.1678 | -0.0232 | 0.0098 | -0.0297 | -0.0241 | -0.0021 |
| EQ42 2483 | 14.1480 | 0.0082 | -0.0074 | -0.0041 | -0.0205 | -0.0161 |
| EQ20 2506A | 16.4030 | 0.0102 | 0.0073 | 0.0061 | 0.0017 | -0.0208 |
| 2498H | 16.6927 | 0.0098 | 0.0068 | 0.0114 | -0.0041 | -0.0197 |
| 2426 | 15.7037 | -0.0318 | -0.0203 | 0.0046 | -0.0291 | -0.0036 |
| EQ44 2498C | 14.3636 | -0.0554 | 0.0079 | 0.0028 | -0.0130 | -0.0079 |
| EQ35 2478 | 15.0577 | -0.0149 | -0.0139 | -0.0229 | -0.0100 | -0.0150 |
| 20059 | 14.9118 | -0.0200 | -0.0091 | -0.0164 | -0.0119 | -0.0153 |
| 10600 | 15.7988 | 0.0168 | -0.0354 | 0.0275 | 0.0057 | 0.0083 |
| 10600 | 13.2345 | 0.0156 | -0.0845 | 0.0001 | -0.0027 | 0.0257 |
| 13/295 | 13.6219 | 0.0245 | 0.0178 | 0.0473 | 0.0020 | -0.0065 |

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|---|---|---|---|---|---|---|
| 13/310 | 15.0071 | 0.0527 | -0.0266 | 0.0208 | -0.0094 | 0.0073 |
| 15/16 | 12.4731 | -0.0430 | 0.0216 | -0.0129 | -0.0900 | 0.0085 |
| 14/35 | 12.0957 | -0.0048 | 0.0453 | 0.0386 | 0.0082 | -0.0165 |
| 14/37 | 13.0017 | -0.0614 | 0.0509 | 0.0039 | -0.0195 | 0.0052 |
| 14/36 | 12.5214 | -0.0696 | 0.0375 | -0.0057 | -0.0519 | -0.0061 |
| 13/02 | 13.1646 | 0.0517 | -0.0200 | -0.0146 | -0.0101 | -0.0278 |
| WCRP 32522 | 15.3581 | -0.0193 | 0.0000 | -0.0378 | -0.0135 | 0.0079 |
| 14/38 | 14.1798 | -0.0600 | 0.0483 | 0.0009 | -0.0323 | -0.0128 |
| 90/16 | 15.6873 | -0.0114 | -0.0041 | 0.0411 | -0.0358 | -0.0024 |
| KNM AB-24280 | 12.8665 | 0.0389 | -0.0097 | 0.0008 | 0.0046 | -0.0132 |
| 1019 | 14.4205 | 0.0115 | 0.0006 | -0.0005 | -0.0069 | 0.0067 |
| 4939 | 14.7262 | 0.0128 | -0.0512 | -0.0236 | -0.0118 | -0.0315 |
| KNM-OG 22833 | 16.8892 | -0.0398 | 0.0417 | 0.0211 | -0.0149 | -0.0133 |
| SAM-AA B6 YSL | 13.5363 | -0.0787 | -0.0033 | -0.0259 | 0.0097 | 0.0732 |
| SR52 | 13.0196 | 0.0757 | 0.0460 | -0.0610 | -0.0247 | -0.0054 |
| SRK32 | 11.3800 | 0.0216 | -0.0268 | -0.0128 | -0.0072 | -0.0187 |
| FLO2778 C1521 | 11.5654 | -0.0271 | -0.0339 | 0.0123 | 0.0145 | -0.0119 |
| VLA115 | 11.5473 | 0.0295 | -0.0182 | -0.0220 | 0.0035 | 0.0173 |
| FLO2638 C1521 | 11.4353 | 0.0038 | -0.0287 | -0.0133 | 0.0075 | -0.0024 |
| FLO2596 C1521 | 11.5443 | -0.0320 | -0.0205 | -0.0016 | 0.0036 | 0.0092 |
| VLA120 | 11.9450 | -0.0211 | -0.0170 | 0.0147 | -0.0053 | 0.0098 |
| FLO2546 C1521 | 12.4881 | 0.0025 | -0.0068 | -0.0004 | 0.0111 | -0.0228 |
| VLA123 | 11.0089 | -0.0247 | -0.0453 | -0.0140 | -0.0100 | -0.0065 |
| VLA116 | 11.8023 | -0.0591 | -0.0219 | -0.0037 | 0.0066 | -0.0094 |
| VLA3 C1521 | 11.3379 | 0.0539 | -0.0027 | -0.0173 | 0.0198 | 0.0073 |
| VLA122 | 10.8006 | -0.0175 | -0.0188 | -0.0102 | -0.0139 | -0.0112 |
| VLA65 C1521 | 11.2892 | 0.1015 | -0.0236 | -0.0232 | -0.0142 | 0.0153 |
| VLA12 C1521 | 11.7407 | 0.0344 | 0.0160 | 0.0011 | -0.0079 | -0.0006 |
| VLA2 C1521 | 10.4752 | 0.0229 | -0.0161 | -0.0415 | 0.0015 | 0.0291 |
| VLA67 C1521 | 10.6646 | -0.0761 | -0.0004 | -0.0231 | -0.0118 | -0.0135 |
| VLA8 C1521 | 12.6585 | 0.0425 | 0.0008 | 0.0251 | 0.0217 | 0.0078 |
| VLA1 C1521 | 11.8199 | -0.0083 | -0.0102 | 0.0172 | -0.0143 | 0.0056 |
| VLA68 C1521 | 11.7915 | 0.0152 | 0.0341 | 0.0045 | -0.0015 | 0.0031 |
| VLA118 | 12.3568 | 0.0171 | -0.0343 | 0.0123 | 0.0306 | 0.0044 |
| VLA6 C1521 | 13.1839 | 0.0011 | -0.0262 | -0.0238 | 0.0279 | -0.0133 |
| VLA59 C1521 | 11.9037 | -0.0417 | 0.0186 | 0.0043 | -0.0096 | -0.0082 |
| VLA17 | 11.2841 | 0.0169 | 0.0032 | -0.0081 | 0.0341 | 0.0133 |
| VLA124 | 11.8382 | 0.0697 | -0.0360 | -0.0007 | 0.0302 | -0.0186 |
| VLA16 C1521 | 11.4795 | 0.0756 | 0.0097 | -0.0314 | 0.0332 | -0.0098 |
| VLA113 | 11.0333 | 0.0500 | -0.0045 | -0.0437 | 0.0227 | -0.0314 |
| VLA117 | 12.0087 | 0.0669 | 0.0080 | -0.0013 | 0.0117 | 0.0226 |
| VLA128 | 11.2439 | 0.0126 | -0.0102 | -0.0358 | 0.0283 | -0.0319 |

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|---|---|---|---|---|---|---|
| VLA11 C1521 | 12.0619 | 0.0563 | 0.0045 | -0.0016 | 0.0288 | -0.0184 |
| FLO2617 C1477 | 11.2480 | 0.0541 | -0.0433 | 0.0121 | -0.0057 | 0.0349 |
| FLO2619 C2784 | 11.9518 | 0.0481 | -0.0444 | -0.0049 | -0.0378 | 0.0081 |
| FLO2560 | 9.7353 | 0.0372 | 0.0343 | -0.0634 | 0.0477 | -0.0447 |
| FLO6061 C1524 | 12.9692 | 0.0749 | 0.0244 | -0.0032 | -0.0242 | -0.0041 |
| FLO6058 C1521 | 11.4525 | -0.0315 | -0.0476 | -0.0415 | -0.0177 | 0.0048 |
| FLO6060 C1521 | 11.4963 | -0.0609 | 0.0553 | -0.0097 | -0.0188 | -0.0656 |
| FLO4878 | 12.6074 | -0.0639 | -0.0035 | -0.0233 | -0.0207 | -0.0204 |
| FLO2767 C1521 | 12.6691 | -0.0692 | -0.0149 | -0.0345 | -0.0155 | -0.0206 |
| FLO1728 C1521 | 11.4712 | -0.0669 | -0.0192 | 0.0100 | -0.0258 | -0.0019 |
| FLO2671 C1521 | 11.2334 | -0.0222 | -0.0012 | -0.0039 | 0.0025 | -0.0038 |
| FLO1726 C1521 | 11.0196 | -0.0278 | -0.0230 | -0.0094 | -0.0141 | -0.0041 |
| FLO2764 C2921 | 10.9774 | 0.0056 | -0.0438 | 0.0112 | -0.0367 | 0.0138 |
| FLO2769 C1521 | 10.4621 | 0.0684 | -0.0274 | -0.0327 | -0.0091 | 0.0277 |
| FLO6047 C1521 | 12.8988 | 0.0018 | -0.0090 | 0.0235 | 0.0302 | -0.0407 |
| FLO6050 C1521 | 11.8472 | 0.0295 | -0.0240 | 0.0160 | 0.0212 | -0.0270 |
| FLO2517 C1521 | 11.1028 | 0.0582 | -0.0271 | 0.0103 | -0.0053 | 0.0110 |
| FLO2783 C1521 | 11.8434 | -0.0310 | -0.0023 | 0.0096 | -0.0063 | -0.0006 |
| PKA 211 | 15.0717 | 0.0065 | -0.0274 | 0.0367 | -0.0431 | -0.0063 |
| PKA 222 | 15.2216 | 0.0072 | 0.0187 | 0.0272 | -0.0272 | -0.0074 |
| PKA 218 | 15.3609 | -0.0326 | 0.0109 | -0.0297 | -0.0608 | -0.0329 |
| PKA 220 | 15.0201 | -0.0368 | 0.0247 | -0.0118 | 0.0072 | -0.0298 |
| 26-323 | 12.3891 | 0.0705 | 0.0535 | -0.0310 | -0.0087 | -0.0157 |
| EC1040 | 12.9737 | 0.0274 | 0.0167 | 0.0051 | 0.0031 | -0.0056 |
| EC1044 | 13.2128 | 0.0259 | 0.0133 | 0.0030 | 0.0296 | 0.0022 |
| EC1045 | 12.3320 | 0.0018 | -0.0256 | -0.0311 | 0.0053 | -0.0185 |
| EC1042 | 12.8536 | 0.0445 | 0.0131 | -0.0120 | -0.0179 | -0.0143 |
| EC1041 | 13.1184 | 0.0372 | 0.0145 | -0.0208 | -0.0181 | 0.0037 |
| EC1039 | 12.7398 | -0.0104 | -0.0019 | -0.0117 | 0.0077 | 0.0000 |
| J19 27-29 | 11.8804 | 0.1965 | 0.0380 | -0.0357 | -0.0575 | -0.0376 |
| EC1037 | 15.8581 | -0.0136 | -0.0165 | 0.0360 | -0.0023 | -0.0171 |
| EC1262 | 12.3357 | 0.0916 | 0.0122 | 0.0150 | -0.0256 | -0.0003 |
| EC108 | 10.8444 | 0.0386 | -0.0472 | -0.0124 | 0.0123 | 0.0041 |
| EC1068 | 10.3407 | 0.0123 | -0.0058 | -0.0238 | -0.0318 | 0.0272 |
| EC1084 | 13.4144 | -0.0172 | -0.0261 | 0.0464 | 0.0136 | -0.0094 |
| EC1083 | 13.3562 | -0.0241 | -0.0312 | 0.0430 | 0.0272 | -0.0109 |
| EC1076 | 13.0124 | 0.0092 | -0.0801 | 0.0136 | 0.0217 | -0.0299 |
| EC902 | 12.0359 | -0.0093 | -0.0229 | -0.0339 | 0.0177 | -0.0157 |
| EC345 | 12.7462 | -0.0049 | 0.0057 | 0.0329 | 0.0137 | -0.0050 |
| EC456 | 12.2845 | 0.0332 | -0.0066 | 0.0263 | 0.0190 | 0.0252 |
| EC340 | 12.6233 | 0.0188 | 0.0100 | -0.0010 | 0.0119 | -0.0194 |
| EC1174 | 12.2843 | 0.0068 | 0.0174 | -0.0134 | -0.0239 | -0.0058 |
| EC286 | 12.1598 | 0.0205 | 0.0115 | -0.0069 | -0.0097 | 0.0120 |

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|---|---|---|---|---|---|---|
| EC454 | 12.7265 | -0.0165 | 0.0440 | 0.0097 | -0.0240 | -0.0354 |
| EC952 | 12.1490 | 0.0108 | -0.0047 | -0.0027 | 0.0061 | -0.0002 |
| EC1024 | 12.6565 | 0.0355 | 0.0059 | -0.0024 | -0.0099 | 0.0241 |
| EC1127 | 13.0888 | 0.0153 | 0.0174 | 0.0088 | -0.0129 | -0.0142 |
| EC1322 | 12.8838 | -0.0237 | 0.0102 | -0.0225 | 0.0132 | 0.0064 |
| EC458 | 11.8983 | -0.0146 | 0.0066 | -0.0202 | -0.0142 | -0.0221 |
| EC298 | 11.8243 | -0.0176 | 0.0210 | 0.0190 | 0.0167 | 0.0202 |
| EC1111 | 12.8481 | 0.0101 | -0.0039 | 0.0069 | 0.0092 | 0.0082 |
| EC147 | 11.7587 | 0.0256 | -0.0098 | -0.0128 | 0.0005 | 0.0322 |
| EC1026 | 12.7636 | 0.0127 | -0.0080 | -0.0090 | -0.0132 | 0.0192 |
| EC1112 | 12.4787 | 0.0392 | -0.0140 | 0.0182 | -0.0403 | -0.0293 |
| EC1149 | 12.0312 | -0.0594 | 0.0163 | 0.0118 | -0.0067 | 0.0008 |
| EC961 | 12.3668 | 0.0067 | 0.0153 | -0.0225 | 0.0104 | 0.0126 |
| EC1157 | 11.9683 | 0.0361 | 0.0083 | -0.0112 | 0.0019 | -0.0062 |
| EC1600 | 12.4818 | -0.0197 | 0.0014 | -0.0126 | -0.0040 | -0.0232 |
| EC1610 | 13.1251 | -0.0123 | 0.0116 | -0.0230 | -0.0206 | -0.0149 |
| EC907 | 12.0755 | -0.0282 | 0.0014 | -0.0006 | -0.0266 | -0.0200 |
| EC453 | 11.9394 | 0.0986 | 0.0007 | -0.0337 | 0.0130 | 0.0251 |
| EC131 | 11.5031 | -0.0456 | -0.0160 | -0.0056 | -0.0138 | 0.0072 |
| EC1056 | 12.7931 | -0.0176 | -0.0376 | -0.0303 | 0.0355 | -0.0115 |
| EC373 | 12.0558 | -0.0331 | -0.0225 | -0.0115 | -0.0159 | -0.0020 |
| EC1259 | 12.0426 | 0.0427 | -0.0826 | -0.0086 | -0.0155 | -0.0037 |
| EC1087 | 14.2355 | -0.0248 | -0.0234 | 0.0251 | -0.0061 | 0.0142 |
| EC330 | 12.7809 | -0.0076 | -0.0161 | 0.0204 | 0.0128 | 0.0169 |
| EC993 | 11.7091 | -0.0216 | -0.0061 | -0.0058 | 0.0057 | 0.0053 |
| EC1197 | 11.6909 | -0.0296 | -0.0224 | 0.0022 | -0.0231 | -0.0030 |
| EC904 | 11.8789 | 0.0969 | -0.0077 | -0.0249 | -0.0180 | 0.0460 |
| EC1261 | 13.9302 | -0.0333 | -0.0230 | 0.0256 | 0.0102 | -0.0180 |
| EC1185 | 11.9466 | 0.0124 | -0.0231 | -0.0118 | 0.0041 | 0.0056 |
| EC1148 | 10.6645 | 0.0415 | -0.0460 | -0.0300 | 0.0214 | 0.0038 |
| EC955 | 11.2965 | -0.0152 | -0.0166 | -0.0104 | 0.0080 | 0.0196 |
| EC1260 | 12.4840 | -0.0124 | -0.0054 | 0.0106 | 0.0028 | 0.0005 |
| EC1267 | 12.0944 | -0.0377 | 0.0034 | -0.0135 | -0.0119 | 0.0071 |
| EC1257 | 12.1197 | -0.0419 | -0.0164 | -0.0020 | -0.0139 | 0.0007 |
| EC1170 | 10.6267 | -0.0045 | -0.0253 | -0.0287 | -0.0194 | 0.0169 |
| EC1080 | 12.5806 | -0.0258 | 0.0019 | -0.0011 | -0.0080 | -0.0021 |
| EC190 | 11.4459 | -0.0338 | 0.0017 | 0.0020 | 0.0048 | 0.0118 |
| EC289 | 11.7296 | -0.0084 | -0.0307 | -0.0510 | -0.0024 | -0.0131 |
| EC335 | 12.1027 | -0.0466 | 0.0030 | 0.0016 | -0.0210 | -0.0066 |
| EC334 | 11.0735 | -0.0011 | -0.0139 | -0.0158 | 0.0000 | 0.0013 |
| EC1169 | 11.2022 | -0.0412 | -0.0125 | -0.0307 | -0.0228 | 0.0083 |
| C2061 | 11.0897 | -0.0218 | -0.0276 | -0.0416 | -0.0249 | -0.0051 |
| C2124 | 16.0874 | -0.0468 | -0.0512 | -0.0127 | -0.0153 | 0.0146 |

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|---|---|---|---|---|---|---|
| C2560 | 12.2175 | 0.0240 | -0.0329 | -0.0080 | -0.0062 | -0.0362 |
| C2115 | 13.2282 | 0.0292 | -0.0082 | 0.0150 | -0.0053 | -0.0610 |
| C2126 | 13.0085 | -0.1171 | 0.0049 | 0.0154 | -0.0240 | 0.0239 |
| C2558 | 12.3032 | -0.0940 | -0.0003 | 0.0038 | -0.0177 | 0.0226 |
| C2560 | 12.3128 | -0.0114 | -0.0133 | 0.0187 | -0.0143 | -0.0344 |
| C2039 | 13.7535 | 0.0181 | 0.0063 | 0.0352 | 0.0076 | -0.0497 |
| C1374 | 15.8517 | -0.0288 | -0.0213 | -0.0074 | -0.0130 | 0.0066 |
| COH10 | 16.4299 | -0.0311 | -0.0261 | 0.0591 | -0.0031 | -0.0091 |
| COH68 | 13.0999 | 0.0117 | -0.0167 | 0.0242 | 0.0001 | 0.0093 |
| COH170 | 12.4987 | -0.0179 | 0.0039 | -0.0082 | 0.0073 | -0.0175 |
| COH161 | 13.2049 | 0.0078 | 0.0109 | 0.0245 | -0.0048 | -0.0211 |
| COH164 | 13.9102 | 0.0131 | -0.0592 | 0.0322 | -0.0140 | -0.0095 |
| COH188 | 13.0463 | -0.0051 | -0.0474 | 0.0130 | 0.0210 | -0.0010 |
| COH136 | 14.7147 | 0.0542 | -0.0056 | 0.0503 | -0.0367 | -0.0213 |
| COH169 | 13.6860 | 0.0209 | 0.0026 | 0.0013 | 0.0292 | -0.0334 |
| N/A | 13.6671 | -0.0178 | -0.0062 | 0.0133 | 0.0096 | -0.0052 |
| COH155 | 13.5966 | 0.0141 | 0.0294 | 0.0180 | 0.0019 | -0.0307 |
| COH276 | 12.0139 | 0.0177 | 0.0082 | 0.0124 | -0.0192 | 0.0153 |
| COH227 | 12.4049 | -0.0604 | 0.0318 | 0.0184 | -0.0120 | 0.0197 |
| COH21-24 | 12.4916 | -0.0307 | 0.0092 | -0.0073 | -0.0144 | -0.0075 |
| COH15-19 | 11.4303 | -0.0357 | -0.0203 | -0.0650 | 0.0283 | -0.0276 |
| COH59 | 15.8626 | 0.0218 | -0.0753 | -0.0124 | -0.0198 | -0.0160 |
| COH18 | 12.6537 | -0.0305 | -0.0212 | -0.0140 | -0.0178 | -0.0134 |
| COH44 | 11.6729 | 0.0549 | -0.0513 | -0.0150 | -0.0055 | -0.0231 |
| COH21 | 12.5741 | -0.0575 | -0.0191 | 0.0081 | -0.0024 | -0.0266 |
| 19 HO | 12.0842 | -0.0301 | -0.0167 | 0.0136 | -0.0085 | 0.0084 |
| COH3 | 13.3176 | -0.0100 | -0.0363 | -0.0033 | 0.0488 | -0.0400 |
| COH173 | 12.6073 | 0.0216 | -0.0092 | -0.0289 | 0.0041 | -0.0030 |
| CD5881 | 15.5132 | -0.0433 | 0.0157 | 0.0030 | 0.0042 | 0.0066 |
| KB561 | 17.4419 | 0.0955 | 0.0141 | 0.0392 | -0.0608 | 0.0540 |
| KB566 | 16.0067 | -0.0207 | -0.0050 | -0.0254 | -0.0263 | 0.0181 |
| 325 | 11.7051 | 0.0708 | 0.0018 | -0.0346 | -0.0097 | 0.0020 |
| 330 | 12.5997 | 0.0307 | -0.0153 | 0.0044 | -0.0175 | 0.0312 |
| KB687 | 12.9307 | 0.0495 | -0.0324 | 0.0353 | -0.0051 | -0.0079 |
| 324 | 11.4302 | -0.0551 | -0.0171 | -0.0241 | 0.0187 | 0.0052 |
| 130 | 12.0025 | -0.0605 | 0.0072 | -0.0125 | -0.0430 | -0.0050 |
| 323 | 12.3473 | 0.1013 | 0.0201 | 0.0188 | -0.0178 | 0.0026 |
| COH163 | 13.8885 | 0.0375 | -0.0470 | -0.0348 | -0.0113 | -0.0221 |
| COH69 | 14.5668 | 0.0409 | -0.0197 | 0.0494 | -0.0350 | -0.0075 |
| COH167 | 13.9262 | 0.0041 | -0.0555 | 0.0195 | -0.0133 | -0.0078 |
| COH160 | 15.5918 | 0.0488 | 0.0053 | 0.0551 | -0.0037 | 0.0060 |
| KB567 | 17.3653 | -0.0220 | -0.0011 | 0.0273 | -0.0194 | 0.0137 |
| KB1565 | 17.7858 | 0.0580 | -0.0109 | 0.0442 | -0.0091 | 0.0200 |

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|---|---|---|---|---|---|---|
| KB45 | 17.0387 | 0.0248 | 0.0284 | -0.0130 | -0.0304 | 0.0059 |
| KB572 | 14.7322 | -0.0336 | 0.0088 | 0.0070 | -0.0134 | 0.0109 |
| KB580 | 15.9585 | -0.0054 | -0.0231 | 0.0016 | -0.0188 | -0.0094 |
| KB563 | 17.4959 | -0.0569 | 0.0210 | 0.0068 | -0.0009 | 0.0057 |
| KB579 | 16.9361 | -0.0858 | -0.0108 | 0.0149 | -0.0431 | -0.0149 |
| 392 | 15.9689 | -0.0272 | -0.0806 | 0.0250 | -0.0459 | -0.0154 |
| KB702 | 11.6606 | 0.0195 | -0.0590 | -0.0265 | -0.0447 | 0.0174 |
| KB653 | 12.1587 | -0.0101 | 0.0166 | -0.0055 | 0.0021 | 0.0054 |
| KB680 | 11.6406 | -0.0325 | -0.0158 | -0.0301 | 0.0290 | -0.0102 |
| KB677 | 13.2259 | -0.0162 | 0.0108 | 0.0115 | 0.0119 | 0.0138 |
| KB685 | 12.3819 | -0.0075 | 0.0344 | 0.0084 | 0.0075 | 0.0016 |
| KB655 | 13.5798 | -0.0117 | 0.0101 | -0.0014 | -0.0196 | -0.0124 |
| KB695 | 12.6446 | 0.0419 | 0.0048 | 0.0102 | -0.0114 | -0.0109 |
| KB700 | 11.8665 | 0.0181 | 0.0052 | -0.0326 | -0.0081 | 0.0120 |
| KB691 | 12.5268 | 0.0010 | -0.0206 | 0.0223 | -0.0225 | 0.0158 |
| KB692 | 11.8805 | -0.0078 | -0.0218 | -0.0060 | 0.0157 | -0.0173 |
| KB659 | 13.1382 | 0.0348 | 0.0330 | 0.0056 | -0.0178 | 0.0152 |
| KB654 | 12.9805 | 0.0589 | -0.0132 | 0.0115 | -0.0184 | -0.0096 |
| KB679 | 10.8920 | -0.0032 | -0.0183 | -0.0198 | 0.0020 | -0.0104 |
| KB672 | 12.1433 | 0.0596 | 0.0336 | -0.0677 | -0.0178 | -0.0372 |
| 359 | 12.2372 | -0.0844 | -0.0216 | -0.0047 | -0.0224 | 0.0025 |
| 328 | 12.6034 | 0.0080 | -0.0319 | 0.0129 | -0.0247 | -0.0247 |
| Pv17790 | 11.1070 | -0.0428 | 0.0157 | -0.0387 | -0.0312 | -0.0341 |
| GV391 B133 | 13.9783 | 0.0496 | -0.0281 | -0.0334 | -0.0200 | -0.0276 |
| COH111 | 11.9207 | 0.0770 | 0.0277 | -0.0319 | -0.0046 | -0.0073 |
| COH141 | 13.0234 | 0.0083 | 0.0033 | 0.0290 | 0.0066 | -0.0271 |
| COH245 | 13.1020 | -0.0952 | -0.0083 | -0.0086 | -0.0158 | -0.0126 |
| BP/4/147 | 13.2230 | -0.0033 | 0.0037 | 0.0899 | 0.0218 | -0.0755 |
| BP/4/911 | 11.3043 | 0.0465 | 0.0368 | -0.0009 | -0.0271 | -0.0361 |
| BP/4/929 | 14.4223 | 0.0298 | 0.0070 | 0.0052 | -0.0391 | -0.0110 |
| EC1082 | 13.3299 | 0.0675 | -0.0188 | 0.0326 | 0.0059 | -0.0563 |

# Appendix D

## Occlusal Enamel Index Measurements

| Catalogue Number | True Area | OEL (mm) | OEI |
|---|---|---|---|
| PKA 211 | 6.625 | 224.878 | 8,736,832,886 |
| PKA 218 | 6.6 | 226.123 | 8,801,825,838 |
| PKA 220 | 6.406 | 220.475 | 8,710,957,284 |
| CD5881 | 6.744 | 243.349 | 9,370,673,047 |
| KB561 | 8.815 | 310.35 | 1,045,299,136 |
| KB566 | 7.328 | 252,149 | 9,314,606,653 |
| COH163 | 5.777 | 248.606 | 1,034,333,098 |
| COH69 | 6.312 | 262.921 | 1,046,506,139 |
| COH167 | 5.567 | 229.981 | 9,747,232,994 |
| COH160 | 7.019 | 259.27 | 9,786,212,603 |
| 392 | 7.527 | 275.308 | 1,003,478,041 |
| GV391-B133 | 5.743 | 258.154 | 1,077,232,507 |
| WCRP 9387 | 6.113 | 235.362 | 9,519,390,617 |
| WCRP 2102 | 6.477 | 257.068 | 1,010,092,323 |
| WCRP 2100 | 6.555 | 236.406 | 923,362,317 |
| WCRP 2110 | 7.319 | 281.957 | 1,042,214,251 |
| WCRP 2049 | 7.921 | 286.393 | 1,017,588,973 |
| 2499A | 7.669 | 280.497 | 1,012,881,996 |
| 2499B | 6.694 | 280.764 | 1,085,171,969 |
| 2499D | 6.082 | 252.757 | 1,024,896,439 |
| 2499C | 6.303 | 253.666 | 1,010,388,995 |
| TEX2619-C | 7.286 | 265.21 | 9,825,288,515 |
| TEX2619-G | 7.788 | 267.492 | 9,585,126,006 |
| TEX2619-B | 6.182 | 235.148 | 9,457,509,559 |
| TEX2619-I-I | 5.928 | 217.623 | 8,938,212,909 |
| TEX2619-I | 6.196 | 228.211 | 9,168,132,253 |
| 2505A | 6.317 | 250.107 | 9,951,084,372 |
| 16799 | 5.522 | 214.468 | 9,126,711,042 |
| 2810 | 5.662 | 256.194 | 1,076,673,495 |
| 1895 | 6.452 | 223.877 | 8,813,781,895 |
| EQ8 2501C | 6.244 | 237.368 | 949,928,075 |
| EQ18 2500A | 5.85 | 225.583 | 9,326,709,178 |
| PKA 222 | 6.669 | 250.613 | 9,704,501,614 |
| COH10 | 7.785 | 268.553 | 9,624,999,149 |
| KB567 | 8.592 | 273.177 | 9,319,594,087 |
| KB1565 | 9.167 | 313.305 | 1,034,793,543 |
| KB45 | 8.891 | 263.916 | 8,850,960,756 |

| | | | |
|---|---|---|---|
| KB572 | 6.253 | 222.417 | 8,894,545,565 |
| KB580 | 7.494 | 256.358 | 9,364,617,223 |
| COH 21-24 | 4.675 | 188.801 | 8,731,995,086 |
| COH 15-19 | 3.731 | 178.398 | 9,235,860,332 |
| COH18 | 4.842 | 204.759 | 9,305,304,888 |
| COH44 | 4.136 | 216.981 | 1,066,918,981 |
| 19HO | 4.135 | 181.328 | 8,917,171,401 |
| 130 | 4.288 | 168.447 | 8,134,594,193 |
| 323 | 4.561 | 213.143 | 9,980,241,217 |
| KB702 | 3.957 | 192.987 | 9,701,637,202 |
| KB653 | 4.32 | 182.008 | 8,756,863,983 |
| KB680 | 4.162 | 173.162 | 8,487,925,427 |
| KB677 | 5.06 | 198.645 | 8,830,847,392 |
| KB685 | 4.654 | 178.914 | 8,293,371,805 |
| KB655 | 5.315 | 210.182 | 9,116,830,613 |
| KB695 | 4.488 | 190.934 | 9,012,740,086 |
| KB691 | 4.734 | 203.715 | 9,362,867,587 |
| KB659 | 4.929 | 206.475 | 930,010,958 |
| KB672 | 4.349 | 188.286 | 9,028,660,555 |
| PV17790 | 3.635 | 151.417 | 7,941,863,707 |
| COH111 | 4.158 | 192.576 | 9,444,085,696 |
| COH141 | 4.691 | 208.217 | 9,613,542,894 |
| KB705 | 3.825 | 165.923 | 848,380,879 |
| KB700 | 4.027 | 183.475 | 9,142,944,459 |
| KB692 | 3.96 | 195.157 | 9,807,008,246 |
| KB654 | 4.947 | 222.726 | 1,001,382,419 |
| KB679 | 3.379 | 160.174 | 8,713,606,134 |
| 359 | 4.034 | 185.427 | 9,232,196,192 |
| 328 | 4.736 | 207.049 | 9,514,090,768 |
| PL17743 | 3.884 | 183.065 | 9,288,930,411 |
| COH245 | 4.897 | 197.502 | 8,924,963,442 |

# Appendix E

## Mesowear Scores

| Catalogue Number | Highest Occlusal Relief (mm) | Cusp Height | Cusp Shape |
|---|---|---|---|
| CAR3 C6 K8-1 1 | 4.13 | High | Round |
| CL4 BBG | 4.51 | High | Round |
| CL3 BGMOU P14 | 1.38 | High | Round |
| CL3 BG Q14 | 1.45 | High | Round |
| WCRP 2110 | 2.15 | High | Round |
| WCRP 2049 | 2.9 | High | Round |
| WCRP 2385 | 2.92 | High | Round |
| WCRP 2102 | 2.86 | High | Round |
| WCRP 2100 | 2.67 | High | Round |
| WCRP 9387 | 2.24 | High | Round |
| WCRP 9389 | 2.77 | High | Round |
| N/A | 3.58 | High | Round |
| 2105 | 3.2 | High | Round |
| EQ18 2500A | 2.63 | High | Round |
| EQ8 2501C | 2.05 | High | Round |
| 2505B | 2.22 | High | Round |
| 2505A | 2.4 | High | Round |
| 9146A | 1.96 | High | Round |
| 16799 | 2.38 | High | Round |
| 2810 | 1.8 | High | Round |
| 1895 | 1.8 | High | Round |
| TEX2619-I | 1.71 | High | Round |
| TEX2619-I-I | 1.79 | High | Round |
| TEX2619-B | 2.33 | High | Round |
| TEX2619-G | 1.84 | High | Round |
| TEX2619-C | 1.44 | High | Round |
| 2499A | 1.66 | High | Round |
| 2499B | 2.6 | High | Round |
| 2499C | 2.13 | High | Round |
| 2499D | 2.29 | High | Round |
| SAM-AA B6 YSL | 1.78 | High | Round |
| SAM-AA D4 YSL | 2.59 | High | Round |
| GV7598 | 2.02 | High | Round |
| GVD1-220 | 3.67 | High | Round |
| GV391-B133 | 2.2 | High | Round |
| GV402 | 2.24 | High | Round |
| PL5854 | 3.51 | High | Round |

| | | | |
|---|---|---|---|
| PL17743 | 1.01 | High | Round |
| PV17790 | 1.88 | High | Round |
| 28881 | 3.24 | High | Round |
| COH160 | 1.43 | High | Round |
| COH127 | 1.02 | High | Round |
| COH167 | 0.7 | Low | Round |
| COH69 | 1.33 | High | Round |
| COH163 | 1.78 | High | Round |
| KB566 | 1.33 | High | Round |
| KB561 | 3.05 | High | Round |
| 323 | 0 | Low | Blunt |
| KB583 | 0.93 | Low | Round |
| KB580 | 1.95 | High | Round |
| KB45 | 2.53 | High | Round |
| KB579 | 1.99 | High | Round |
| KB581 | 2.47 | High | Round |
| KB1565 | 1.31 | High | Round |
| KB567 | 3.1 | High | Round |
| KB45 | 0 | Low | Blunt |
| KB572 | 2.59 | High | Round |
| 390 | 2.9 | High | Round |
| 392 | 1.5 | High | Round |
| KB653 | 1.34 | High | Round |
| KB704 | 2.15 | High | Round |
| KB676 | 1.39 | High | Round |
| KB702 | 1.74 | High | Round |
| KB680 | 2.1 | High | Round |
| KB677 | 2.24 | High | Round |
| KB685 | 1.93 | High | Round |
| KB700 | 1.67 | High | Round |
| KB654 | 1.45 | High | Round |
| KB691 | 1.88 | High | Round |
| KB655 | 1.36 | High | Round |
| KB705 | 1.4 | High | Round |
| KB659 | 2.15 | High | Round |
| KB692 | 1.19 | High | Round |
| KB695 | 2 | High | Round |
| KB679 | 2.22 | High | Round |
| KB672 | 1.72 | High | Round |
| 328 | 1.83 | High | Round |
| 359 | 2.02 | High | Round |
| CD5881 | 2.7 | High | Round |
| CD9293 | 3.1 | High | Round |

| | | | |
|---|---|---|---|
| COH68 | 2.13 | High | Round |
| COH170 | 3.01 | High | Round |
| COH161 | 2.23 | High | Round |
| COH276 | 2.36 | High | Round |
| COH227 | 0.88 | High | Round |
| COH169 | 2.11 | High | Round |
| COH360 | 1 | Low | Round |
| COH164 | 2.02 | High | Round |
| COH188 | 1.29 | High | Round |
| COH136 | 1.31 | High | Round |
| COH28 | 2.17 | High | Round |
| COH155 | 1.5 | High | Round |
| N/A | 1.82 | High | Round |
| COH21-24 | 1.99 | High | Round |
| COH15-19 | 1.29 | High | Round |
| COH3 | 1.57 | High | Round |
| COH134 | 1.41 | High | Round |
| COH173 | 2.74 | High | Round |
| COH370 | 2.8 | High | Round |
| COH10 | 2.49 | High | Round |
| COH53 | 1.78 | High | Round |
| COH59 | 2.57 | High | Round |
| COH27 | 1.04 | High | Round |
| COH54 | 2.08 | High | Round |
| COH5 | 3.25 | High | Round |
| COH18 | 1.53 | High | Round |
| COH44 | 2.45 | High | Round |
| 19HO | 2.59 | High | Round |
| COH245 | 2.29 | High | Round |
| COH165 | 1.8 | High | Round |
| COH111 | 2.51 | High | Round |
| COH111 | 1.87 | High | Round |
| COH130 | 1.48 | High | Round |
| COH141 | 1.59 | High | Round |
| COH594 | 0.74 | Low | Round |
| PKA218 | 2.4 | High | Round |
| PKA216 | 1.16 | High | Round |
| PKA211 | 1.53 | High | Round |
| PKA222 | 3.2 | High | Round |
| PKA213 | 2.03 | High | Round |
| PKA217 | 1.72 | High | Round |
| PKA220 | 1.96 | High | Round |
| PKA221 | 1.7 | High | Round |

# Appendix F

## Specimen Details

| Assigned Species | Catalogue Number | Site | Side | Jaw | Curated | GMM | LM | OEI | Mesowear |
|---|---|---|---|---|---|---|---|---|---|
| *Equus* | C2123 | MAHEMSPAN | Right | Lower | University of the Witswaterstrand | Yes | No | No | No |
| *Equus* | C2121 | MAHEMSPAN | Right | Lower | University of the Witswaterstrand | Yes | No | No | No |
| *Equus* | C1775 | MAHEMSPAN | Right | Lower | University of the Witswaterstrand | Yes | No | No | No |
| *Equus* | C1973 | MAHEMSPAN | Right | Lower | University of the Witswaterstrand | Yes | No | No | No |
| *Equus* | C2119 | MAHEMSPAN | Right | Lower | University of the Witswaterstrand | Yes | No | No | No |
| *Equus* | Unmarked | CALVINIA | Right | Lower | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | EC1277 | EQUUS CAVE | Left | Lower | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | EC1276 | EQUUS CAVE | Right | Lower | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | EC1273 | EQUUS CAVE | Left | Lower | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | EC1008 | EQUUS CAVE | Left | Lower | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | EC934 | EQUUS CAVE | Left | Lower | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | EC1173 | EQUUS CAVE | Right | Lower | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | EC500 | EQUUS CAVE | Left | Lower | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | EC1274 | EQUUS CAVE | Left | Lower | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | EC1186 | EQUUS CAVE | Right | Lower | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | EC378 | EQUUS CAVE | Left | Lower | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | EC499 | EQUUS CAVE | Right | Lower | Florisbad Quaternary Research Station | Yes | No | No | No |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| *Equus* | EC1275 | EQUUS CAVE | Right | Lower | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | EC959 | EQUUS CAVE | Right | Lower | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | EC1071 | EQUUS CAVE | Right | Lower | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | EC1283 | EQUUS CAVE | Right | Lower | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | EC1208 | EQUUS CAVE | Right | Lower | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | EC1199 | EQUUS CAVE | Right | Lower | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | EC1017 | EQUUS CAVE | Right | Lower | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | EC1098 | EQUUS CAVE | Right | Lower | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | EC1275 | EQUUS CAVE | Left | Lower | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | EC1281 | EQUUS CAVE | Left | Lower | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | EC1016 | EQUUS CAVE | Left | Lower | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | EC971 | EQUUS CAVE | Right | Lower | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | EC396 | EQUUS CAVE | Left | Lower | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | EC1022 | EQUUS CAVE | Right | Lower | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | EC1168 | EQUUS CAVE | Left | Lower | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | EC2 | EQUUS CAVE | Left | Lower | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | EC400 | EQUUS CAVE | Right | Lower | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | EC1025 | EQUUS CAVE | Left | Lower | Florisbad Quaternary Research Station | Yes | No | No | No |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| *Equus* | EC1069 | EQUUS CAVE | Right | Lower | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | EC216 | EQUUS CAVE | Right | Lower | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | EC1278 | EQUUS CAVE | Right | Lower | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | EC1021 | EQUUS CAVE | Right | Lower | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | EC1055 | EQUUS CAVE | Left | Lower | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | J19 8 | EQUUS CAVE | Left | Lower | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | VLA130 C1522 | VLAKRAAL | Left | Lower | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | VLA85 C1522 | VLAKRAAL | Right | Lower | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | VLA75 FLO4873 | VLAKRAAL | Left | Lower | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | VLA28 C1522 | VLAKRAAL | Left | Lower | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | VLA77 C1522 | VLAKRAAL | Left | Lower | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | VLA72 C1522 | VLAKRAAL | Left | Lower | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | VLA19 C1522 | VLAKRAAL | Right | Lower | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | SR4-9 | SAND RIVER | Right | Lower | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | SR41 | SAND RIVER | Left | Lower | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | 20970K | ELANDSFONTEIN | Left | Lower | Iziko South African museum | Yes | No | No | No |
| *Equus* | 2504A | ELANDSFONTEIN | Right | Lower | Iziko South African museum | Yes | No | No | No |
| *Equus* | 20974C | ELANDSFONTEIN | Left | Lower | Iziko South African museum | Yes | No | No | No |
| *Equus* | TEX2625 | ELANDSFONTEIN | Left | Lower | Iziko South African museum | Yes | No | No | No |
| *Equus* | 2174 | ELANDSFONTEIN | Right | Lower | Iziko South African museum | Yes | No | No | No |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| *Equus* | 20974B | ELANDSFONTEIN | Left | Lower | Iziko South African museum | Yes | No | No | No |
| *Equus* | Unmarked | ELANDSFONTEIN | Left | Lower | Iziko South African museum | Yes | No | No | No |
| *Equus* | 16864 | ELANDSFONTEIN | Left | Lower | Iziko South African museum | Yes | No | No | No |
| *Equus* | 15829 | ELANDSFONTEIN | Left | Lower | Iziko South African museum | Yes | No | No | No |
| *Equus* | 2205 | ELANDSFONTEIN | Left | Lower | Iziko South African museum | Yes | No | No | No |
| *Equus* | 10601 | ELANDSFONTEIN | Right | Lower | Iziko South African museum | Yes | No | No | No |
| *Equus* | 10602 | ELANDSFONTEIN | Left | Lower | Iziko South African museum | Yes | No | No | No |
| *Equus* | FLO2700 C1522 | FLORISBAD | Right | Lower | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | FLO4617 C1522 | FLORISBAD | Right | Lower | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | FLO6027 C1582 | FLORISBAD | Right | Lower | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | FLO6029 C1484 | FLORISBAD | Right | Lower | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | FLO6030 C1522 | FLORISBAD | Right | Lower | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | FLO6024 | FLORISBAD | Left | Lower | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | FLO6023 C1522 | FLORISBAD | Left | Lower | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | FLO6053 SAM10622 | FLORISBAD | Right | Lower | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | FLO6025 C1522 | FLORISBAD | Right | Lower | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | FLO2545 C2609 | FLORISBAD | Right | Lower | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | FLO6026 C1522 | FLORISBAD | Left | Lower | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | FLO2583 C2602 | FLORISBAD | Left | Lower | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | FLO6033 C1522 | FLORISBAD | Right | Lower | Florisbad Quaternary Research Station | Yes | No | No | No |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| *Equus* | FLO6011 C1522 | FLORISBAD | Right | Lower | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | FLO6010 C1522 | FLORISBAD | Right | Lower | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | FLO6045 C1522 | FLORISBAD | Left | Lower | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | FLO6035 C1522 | FLORISBAD | Left | Lower | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | FLO6038 C1522 | FLORISBAD | Right | Lower | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | FLO6034 C1522 | FLORISBAD | Right | Lower | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | FLO6014 C1522 | FLORISBAD | Left | Lower | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | FLO6009 C1522 | FLORISBAD | Left | Lower | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | FLO6028 | FLORISBAD | Left | Lower | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus caballus* | BP/4/152 | (MODERN) | Left | Lower | University of Cape Town | Yes | No | No | No |
| *Equus caballus* | BP/4/929 | (MODERN) | Left | Lower | University of Cape Town | Yes | No | No | No |
| *Equus caballus* | 13/295 | (MODERN) | Left | Lower | University of Cape Town | Yes | No | No | No |
| *Equus caballus* | 90/16 | (MODERN) | Left | Lower | University of Cape Town | Yes | No | No | No |
| *Equus zebra* | 14/35 | (MODERN) | Left | Lower | University of Cape Town | Yes | No | No | No |
| *Equus zebra* | 14/37 | (MODERN) | Right | Lower | University of Cape Town | Yes | No | No | No |
| *Equus asinus* | 11/19 | (MODERN) | Left | Lower | University of Cape Town | Yes | No | No | No |
| *Equus capensis* | CAR3 C6 K8-1 2 | ELANDS BAY CAVE | Left | Lower | Iziko South African museum | No | Yes | No | No |
| *Equus capensis* | CAR3 C6 K8-1 3 | ELANDS BAY CAVE | Right | Lower | Iziko South African museum | Yes | Yes | No | No |
| *Equus capensis* | GBAN F5 | ELANDS BAY CAVE | Left | Lower | Iziko South African museum | Yes | Yes | No | No |
| *Equus capensis* | CL3 015 | BOOMPLAAS | Left | Lower | Iziko South African museum | No | Yes | No | No |
| *Equus capensis* | CL3 BP Q15 | BOOMPLAAS | Left | Lower | Iziko South African museum | No | Yes | No | No |
| *Equus capensis* | Q34A | ELANDSFONTEIN | Left | Lower | Iziko South African museum | Yes | Yes | No | No |
| *Equus capensis* | 6634 | ELANDSFONTEIN | Left | Lower | Iziko South African museum | Yes | Yes | No | No |

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|---|---|---|---|---|---|---|---|---|---|
| *Equus capensis* | 209705 | ELANDSFONTEIN | Left | Lower | Iziko South African museum | Yes | Yes | No | No |
| *Equus capensis* | 209700 | ELANDSFONTEIN | Right | Lower | Iziko South African museum | No | Yes | No | No |
| *Equus capensis* | 2206 | ELANDSFONTEIN | Left | Lower | Iziko South African museum | Yes | Yes | No | No |
| *Equus capensis* | 3899-C | ELANDSFONTEIN | Left | Lower | Iziko South African museum | Yes | Yes | No | No |
| *Equus capensis* | 1894 | ELANDSFONTEIN | Left | Lower | Iziko South African museum | Yes | Yes | No | No |
| *Equus capensis* | 1970 | ELANDSFONTEIN | Left | Lower | Iziko South African museum | Yes | Yes | No | No |
| *Equus capensis* | 10068F | ELANDSFONTEIN | Right | Lower | Iziko South African museum | No | Yes | No | No |
| *Equus capensis* | 10068B | ELANDSFONTEIN | Right | Lower | Iziko South African museum | No | Yes | No | No |
| *Equus capensis* | 10068C | ELANDSFONTEIN | Right | Lower | Iziko South African museum | No | Yes | No | No |
| *Equus capensis* | 10068A | ELANDSFONTEIN | Right | Lower | Iziko South African museum | Yes | Yes | No | No |
| *Equus capensis* | 20971A | ELANDSFONTEIN | Left | Lower | Iziko South African museum | No | Yes | No | No |
| *Equus capensis* | 17562 | ELANDSFONTEIN | Left | Lower | Iziko South African museum | Yes | Yes | No | No |
| *Equus capensis* | 11414 | ELANDSFONTEIN | Left | Lower | Iziko South African museum | Yes | Yes | No | No |
| *Equus capensis* | GV5350 | GLADYSVALE | Right | Lower | University of the Witswaterstrand | No | Yes | No | No |
| *Equus capensis* | GVL1-115-B1 | GLADYSVALE | Right | Lower | University of the Witswaterstrand | No | Yes | No | No |
| *Equus capensis* | GV7961 | GLADYSVALE | Left | Lower | University of the Witswaterstrand | Yes | Yes | No | No |
| *Equus capensis* | GV4523 | GLADYSVALE | Right | Lower | University of the Witswaterstrand | No | Yes | No | No |
| *Equus capensis* | GVD1-104-B24 | GLADYSVALE | Left | Lower | University of the Witswaterstrand | No | Yes | No | No |
| *Equus capensis* | 42258 | SWARTKRANS | Left | Lower | University of the Witswaterstrand | Yes | Yes | No | No |
| *Equus capensis* | 31932 | SWARTKRANS | Left | Lower | University of the Witswaterstrand | No | Yes | No | No |
| *Equus capensis* | 19616 | SWARTKRANS | Right | Lower | University of the Witswaterstrand | No | Yes | No | No |
| *Equus capensis* | 36437 | SWARTKRANS | Left | Lower | University of the Witswaterstrand | No | Yes | No | No |
| *Equus capensis* | COH650 | MAKAPANSGAT | Right | Lower | University of the Witswaterstrand | No | Yes | No | No |
| *Equus capensis* | COH440 | MAKAPANSGAT | Right | Lower | University of the Witswaterstrand | No | Yes | No | No |
| *Equus capensis* | KB594 | KALKBANK | Right | Lower | University of the Witswaterstrand | No | Yes | No | No |
| *Equus capensis* | KB595 | KALKBANK | Left | Lower | University of the Witswaterstrand | Yes | Yes | No | No |
| *Equus capensis* | COH553 | CAVE OF HEARTHS | Left | Lower | University of the Witswaterstrand | No | Yes | No | No |

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|---|---|---|---|---|---|---|---|---|---|
| *Equus capensis* | COH24-25 | CAVE OF HEARTHS | Left | Lower | University of the Witswaterstrand | Yes | Yes | No | No |
| *Equus capensis* | COH415 | CAVE OF HEARTHS | Right | Lower | University of the Witswaterstrand | Yes | Yes | No | No |
| *Equus capensis* | COH550 | CAVE OF HEARTHS | Right | Lower | University of the Witswaterstrand | Yes | Yes | No | No |
| *Equus capensis* | COH495 | CAVE OF HEARTHS | Right | Lower | University of the Witswaterstrand | Yes | Yes | No | No |
| *Equus capensis* | COH497 | CAVE OF HEARTHS | Left | Lower | University of the Witswaterstrand | No | Yes | No | No |
| *Equus capensis* | COH404 | CAVE OF HEARTHS | Left | Lower | University of the Witswaterstrand | Yes | Yes | No | No |
| *Equus capensis* | PK A210 | SPITSKOP | Left | Lower | Florisbad Quaternary Research Station | Yes | Yes | No | No |
| *Equus capensis* | P28 19A | BYNESKRANSKOP | Left | Lower | Iziko South African museum | Yes | Yes | No | No |
| *Equus aff. capensis* | 372 | OLORGESAILIE | Left | Lower | National Museums of Kenya | Yes | No | No | No |
| *Equus aff. capensis* | 4940 | OLORGESAILIE | Right | Lower | National Museums of Kenya | Yes | No | No | No |
| *Equus aff. capensis* | 5373 | OLORGESAILIE | Left | Lower | National Museums of Kenya | Yes | No | No | No |
| *Equus capensis/quagga* | COH557 | CAVE OF HEARTHS | Left | Lower | University of the Witswaterstrand | No | Yes | No | No |
| *Equus capensis/quagga* | COH442 | CAVE OF HEARTHS | Left | Lower | University of the Witswaterstrand | Yes | Yes | No | No |
| *Equus grevyi* | KAR12-219 | KISAAKA | Right | Lower | National Museums of Kenya | No | Yes | No | No |
| *Equus grevyi* | KAR12-140 | KISAAKA | Right | Lower | National Museums of Kenya | Yes | Yes | No | No |
| *Equus grevyi* | KAR12-271 | KISAAKA | Right | Lower | National Museums of Kenya | Yes | Yes | No | No |
| *Equus grevyi* | KNM-AB 24228 | AMBOSELI | Right | Lower | National Museums of Kenya | Yes | Yes | No | No |
| *Equus lylei* | FLO2501 C1479 | FLORISBAD | Left | Lower | Florisbad Quaternary Research Station | Yes | Yes | No | No |
| *Equus lylei* | FLO4866 | FLORISBAD | Right | Lower | Florisbad Quaternary Research Station | No | Yes | No | No |
| *Equus lylei* | FLO6013 C2921 | FLORISBAD | Right | Lower | Florisbad Quaternary Research Station | No | Yes | No | No |
| *Equus lylei* | FLO6006 C1522 | FLORISBAD | Left | Lower | Florisbad Quaternary Research Station | Yes | Yes | No | No |

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|---|---|---|---|---|---|---|---|---|---|
| *Equus lylei* | FLO6004 C2921 | FLORISBAD | Right | Lower | Florisbad Quaternary Research Station | Yes | Yes | No | No |
| *Equus lylei* | FLO6051 SAM10622 | FLORISBAD | Right | Lower | Florisbad Quaternary Research Station | Yes | Yes | No | No |
| *Equus lylei* | FLO2568 | FLORISBAD | Right | Lower | Florisbad Quaternary Research Station | Yes | Yes | No | No |
| *Equus lylei* | FLO6001 C1522 | FLORISBAD | Right | Lower | Florisbad Quaternary Research Station | No | Yes | No | No |
| *Equus lylei* | FLO4635 C1522 | FLORISBAD | Left | Lower | Florisbad Quaternary Research Station | Yes | Yes | No | No |
| *Equus lylei* | FLO4608 C1522 | FLORISBAD | Left | Lower | Florisbad Quaternary Research Station | Yes | Yes | No | No |
| *Equus lylei* | FLO2609 | FLORISBAD | Left | Lower | Florisbad Quaternary Research Station | Yes | Yes | No | No |
| *Equus lylei* | FLO2562 C1484 | FLORISBAD | Left | Lower | Florisbad Quaternary Research Station | Yes | Yes | No | No |
| *Equus lylei* | FLO2571 C1484 | FLORISBAD | Left | Lower | Florisbad Quaternary Research Station | No | Yes | No | No |
| *Equus lylei* | FLO6055 SAM10622 | FLORISBAD | Right | Lower | Florisbad Quaternary Research Station | Yes | Yes | No | No |
| *Equus lylei* | FLO6052 SAM10622 | FLORISBAD | Right | Lower | Florisbad Quaternary Research Station | Yes | Yes | No | No |
| *Equus lylei* | FLO2579 | FLORISBAD | Right | Lower | Florisbad Quaternary Research Station | Yes | Yes | No | No |
| *Equus quagga* | 13/198 | (MODERN) | Right | Lower | University of Cape Town | Yes | No | No | No |
| *Equus quagga* | PV12004 | PLOVERS LAKE | Left | Lower | University of the Witswaterstrand | Yes | Yes | No | No |
| *Equus quagga* | KB618 | KALKBANK | Left | Lower | University of the Witswaterstrand | Yes | Yes | No | No |
| *Equus quagga* | KNM-AB 24231 | AMBOSELI | Left | Lower | National Museums of Kenya | Yes | No | No | No |
| *Equus quagga* | 379 | KALKBANK | Left | Lower | University of the Witswaterstrand | No | Yes | No | No |
| *Equus quagga* | 371 | KALKBANK | Right | Lower | University of the Witswaterstrand | No | Yes | No | No |
| *Equus quagga* | 376 | KALKBANK | Right | Lower | University of the Witswaterstrand | Yes | Yes | No | No |
| *Equus quagga* | 372 | KALKBANK | Left | Lower | University of the Witswaterstrand | Yes | Yes | No | No |
| *Equus quagga* | 377 | KALKBANK | Left | Lower | University of the Witswaterstrand | Yes | Yes | No | No |

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|---|---|---|---|---|---|---|---|---|---|
| *Equus quagga* | COH Tu/15-19/28-30 | CAVE OF HEARTHS | Left | Lower | University of the Witswaterstrand | No | Yes | No | No |
| *Equus quagga* | COH Tu/15-19 | CAVE OF HEARTHS | Left | Lower | University of the Witswaterstrand | Yes | Yes | No | No |
| *Equus quagga* | COH28-30 | CAVE OF HEARTHS | Right | Lower | University of the Witswaterstrand | Yes | Yes | No | No |
| *Equus quagga* | COH548 | CAVE OF HEARTHS | Right | Lower | University of the Witswaterstrand | No | Yes | No | No |
| *Equus quagga* | COH590 | CAVE OF HEARTHS | Left | Lower | University of the Witswaterstrand | Yes | Yes | No | No |
| *Equus quagga* | COH582 | CAVE OF HEARTHS | Right | Lower | University of the Witswaterstrand | Yes | Yes | No | No |
| *Equus quagga* | COH594 | CAVE OF HEARTHS | Right | Lower | University of the Witswaterstrand | Yes | No | No | No |
| *Equus quagga* | COH472 | CAVE OF HEARTHS | Right | Lower | University of the Witswaterstrand | Yes | Yes | No | No |
| *Equus quagga* | KAR13-110 | KISAAKA | Right | Lower | National Museums of Kenya | Yes | No | No | No |
| *Equus quagga* | KAR12-134 | KISAAKA | Left | Lower | National Museums of Kenya | Yes | No | No | No |
| *Equus quagga* | KAR12-47 | ONGE | Right | Lower | National Museums of Kenya | Yes | No | No | No |
| *Equus quagga* | BP/4/147 | (MODERN) | Left | Lower | University of Cape Town | Yes | No | No | No |
| *Equus quagga* | BP/4/911 | (MODERN) | Right | Lower | University of Cape Town | Yes | No | No | No |
| *Equus zebra* | CL1L | BOOMPLAAS | Right | Lower | Iziko South African museum | No | Yes | No | No |
| *Equus zebra* | CL2 P12 | BOOMPLAAS | Left | Lower | Iziko South African museum | No | Yes | No | No |
| *Equus zebra* | CL1 N15 | BOOMPLAAS | Right | Lower | Iziko South African museum | Yes | Yes | No | No |
| *Equus zebra* | BPL4 016 | BOOMPLAAS | Left | Lower | Iziko South African museum | No | Yes | No | No |
| *Equus zebra* | 13/02 | (MODERN) | Right | Lower | University of Cape Town | Yes | No | No | No |
| *Equus zebra* | 14/38 | (MODERN) | Left | Lower | University of Cape Town | Yes | No | No | No |
| *Equus capensis* | CAR3 C6 K8-1 1 | ELANDS BAY CAVE | Left | Upper | Iziko South African museum | No | Yes | No | Yes |
| *Equus capensis* | CL4 BBG | BOOMPLAAS | Left | Upper | Iziko South African museum | No | Yes | No | Yes |
| *Equus zebra* | CL1 | BOOMPLAAS | Left | Upper | Iziko South African museum | No | Yes | No | No |
| *Equus capensis* | CL3 P14 | BOOMPLAAS | Left | Upper | Iziko South African museum | No | Yes | No | No |
| *Equus capensis* | CL3 BGMOU P14 | BOOMPLAAS | Right | Upper | Iziko South African museum | No | Yes | No | Yes |
| *Equus capensis* | CL3 BG Q14 | BOOMPLAAS | Right | Upper | Iziko South African museum | No | Yes | No | Yes |
| *Equus capensis* | WCRP 2110 | ELANDSFONTEIN | Right | Upper | University of Cape Town | Yes | Yes | Yes | Yes |

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|---|---|---|---|---|---|---|---|---|---|
| *Equus capensis* | WCRP 2049 | ELANDSFONTEIN | Left | Upper | University of Cape Town | Yes | Yes | Yes | Yes |
| *Equus capensis* | WCRP 2385 | ELANDSFONTEIN | Right | Upper | University of Cape Town | Yes | Yes | No | Yes |
| *Equus capensis* | WCRP 2102 | ELANDSFONTEIN | Left | Upper | University of Cape Town | Yes | Yes | Yes | Yes |
| *Equus capensis* | WCRP 2100 | ELANDSFONTEIN | Left | Upper | University of Cape Town | Yes | Yes | Yes | Yes |
| *Equus capensis* | WCRP 9387 | ELANDSFONTEIN | Left | Upper | University of Cape Town | Yes | Yes | Yes | Yes |
| *Equus* | WCRP 32522 | ELANDSFONTEIN | Left | Upper | University of Cape Town | Yes | No | No | No |
| *Equus capensis* | WCRP 9389 | ELANDSFONTEIN | Left | Upper | University of Cape Town | Yes | Yes | No | Yes |
| *Equus capensis* | N/A | ELANDSFONTEIN | Right | Upper | Iziko South African museum | Yes | Yes | No | Yes |
| *Equus* | EQ28 2472 | ELANDSFONTEIN | Left | Upper | Iziko South African museum | Yes | No | No | No |
| *Equus* | 16772 (46) | ELANDSFONTEIN | Right | Upper | Iziko South African museum | Yes | No | No | No |
| *Equus* | 2590 | ELANDSFONTEIN | Left | Upper | Iziko South African museum | Yes | No | No | No |
| *Equus* | EQ48 2498B | ELANDSFONTEIN | Right | Upper | Iziko South African museum | Yes | No | No | No |
| *Equus* | EQ52 2490 | ELANDSFONTEIN | Left | Upper | Iziko South African museum | Yes | No | No | No |
| *Equus* | 6726 | ELANDSFONTEIN | Right | Upper | Iziko South African museum | Yes | No | No | No |
| *Equus* | EQ51 2498E | ELANDSFONTEIN | Left | Upper | Iziko South African museum | Yes | No | No | No |
| *Equus* | EQ31 2474 | ELANDSFONTEIN | Left | Upper | Iziko South African museum | Yes | No | No | No |
| *Equus* | EQ2466 | ELANDSFONTEIN | Left | Upper | Iziko South African museum | Yes | No | No | No |
| *Equus* | EQ2456 | ELANDSFONTEIN | Left | Upper | Iziko South African museum | Yes | No | No | No |
| *Equus* | 5352E | ELANDSFONTEIN | Left | Upper | Iziko South African museum | Yes | No | No | No |
| *Equus* | 20798 | ELANDSFONTEIN | Right | Upper | Iziko South African museum | Yes | No | No | No |
| *Equus* | EQ42 2483 | ELANDSFONTEIN | Left | Upper | Iziko South African museum | Yes | No | No | No |
| *Equus* | EQ20 2506A | ELANDSFONTEIN | Left | Upper | Iziko South African museum | Yes | No | No | No |
| *Equus* | 2498H | ELANDSFONTEIN | Left | Upper | Iziko South African museum | Yes | No | No | No |
| *Equus* | 2426 | ELANDSFONTEIN | Right | Upper | Iziko South African museum | Yes | No | No | No |
| *Equus* | EQ44 2498C | ELANDSFONTEIN | Right | Upper | Iziko South African museum | Yes | No | No | No |
| *Equus* | EQ35 2478 | ELANDSFONTEIN | Right | Upper | Iziko South African museum | Yes | No | No | No |
| *Equus* | 20059 | ELANDSFONTEIN | Right | Upper | Iziko South African museum | Yes | No | No | No |

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|---|---|---|---|---|---|---|---|---|---|
| *Equus* | 16660C | ELANDSFONTEIN | Right | Upper | Iziko South African museum | Yes | No | No | No |
| *Equus* | 16661E | ELANDSFONTEIN | Left | Upper | Iziko South African museum | Yes | No | No | No |
| *Equus* | 16660E | ELANDSFONTEIN | Right | Upper | Iziko South African museum | Yes | No | No | No |
| *Equus* | 17257 | ELANDSFONTEIN | Right | Upper | Iziko South African museum | Yes | No | No | No |
| *Equus capensis* | 2105 | ELANDSFONTEIN | Left | Upper | Iziko South African museum | Yes | Yes | No | Yes |
| *Equus capensis* | EQ18 2500A | ELANDSFONTEIN | Left | Upper | Iziko South African museum | Yes | Yes | Yes | Yes |
| *Equus capensis* | EQ8 2501C | ELANDSFONTEIN | Right | Upper | Iziko South African museum | Yes | Yes | Yes | Yes |
| *Equus capensis* | 2505B | ELANDSFONTEIN | Right | Upper | Iziko South African museum | No | Yes | No | Yes |
| *Equus capensis* | 2505A | ELANDSFONTEIN | Right | Upper | Iziko South African museum | Yes | Yes | Yes | Yes |
| *Equus capensis* | 9146A | ELANDSFONTEIN | Right | Upper | Iziko South African museum | Yes | Yes | No | Yes |
| *Equus capensis* | 16799 | ELANDSFONTEIN | Right | Upper | Iziko South African museum | Yes | Yes | Yes | Yes |
| *Equus capensis* | 2810 | ELANDSFONTEIN | Left | Upper | Iziko South African museum | Yes | Yes | Yes | Yes |
| *Equus capensis* | 1895 | ELANDSFONTEIN | Right | Upper | Iziko South African museum | Yes | Yes | Yes | Yes |
| *Equus capensis* | TEX2619-I | ELANDSFONTEIN | Left | Upper | Iziko South African museum | Yes | Yes | Yes | Yes |
| *Equus capensis* | TEX2619-I-I | ELANDSFONTEIN | Left | Upper | Iziko South African museum | Yes | Yes | Yes | Yes |
| *Equus capensis* | TEX2619-B | ELANDSFONTEIN | Right | Upper | Iziko South African museum | Yes | Yes | Yes | Yes |
| *Equus capensis* | TEX2619-G | ELANDSFONTEIN | Left | Upper | Iziko South African museum | Yes | Yes | Yes | Yes |
| *Equus capensis* | TEX2619-C | ELANDSFONTEIN | Right | Upper | Iziko South African museum | Yes | Yes | Yes | Yes |
| *Equus capensis* | 2499A | ELANDSFONTEIN | Left | Upper | Iziko South African museum | Yes | Yes | Yes | Yes |
| *Equus capensis* | 2499B | ELANDSFONTEIN | Left | Upper | Iziko South African museum | Yes | Yes | Yes | Yes |
| *Equus capensis* | 2499C | ELANDSFONTEIN | Left | Upper | Iziko South African museum | Yes | Yes | Yes | Yes |
| *Equus capensis* | 2499D | ELANDSFONTEIN | Left | Upper | Iziko South African museum | Yes | Yes | Yes | Yes |
| *Equus* | 10600 | ELANDSFONTEIN | Left | Upper | Iziko South African museum | Yes | No | No | No |
| *Equus* | 10600 | ELANDSFONTEIN | Left | Upper | Iziko South African museum | Yes | No | No | No |
| *Equus asinus* | BP/4/149 | (MODERN) | Right | Upper | University of Cape Town | No | Yes | No | No |
| *Equus quagga*(zebra) | BP/4/147 | (MODERN) | Left | Upper | University of Cape Town | Yes | Yes | No | No |
| *Equus quagga*(zebra) | BP/4/911 | (MODERN) | Left | Upper | University of Cape Town | Yes | Yes | No | No |

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|---|---|---|---|---|---|---|---|---|---|
| *Equus caballus* | BP/4/929 | (MODERN) | Left | Upper | University of Cape Town | Yes | No | No | No |
| *Equus caballus* | 13/295 | (MODERN) | Left | Upper | University of Cape Town | Yes | No | No | No |
| *Equus caballus* | 13/310 | (MODERN) | Left | Upper | University of Cape Town | Yes | No | No | No |
| *Equus zebra* | 15/16 | (MODERN) | Left | Upper | University of Cape Town | Yes | Yes | No | No |
| *Equus zebra* | 14/35 | (MODERN) | Right | Upper | University of Cape Town | Yes | Yes | No | No |
| *Equus zebra* | 14/37 | (MODERN) | Left | Upper | University of Cape Town | Yes | Yes | No | No |
| *Equus zebra* | 14/36 | (MODERN) | Left | Upper | University of Cape Town | Yes | Yes | No | No |
| *Equus zebra* | 13/02 | (MODERN) | Left | Upper | University of Cape Town | Yes | Yes | No | No |
| *Equus asinus* | 11/19 | (MODERN) | Left | Upper | University of Cape Town | No | Yes | No | No |
| *Equus caballus* | 90/16 | (MODERN) | Right | Upper | University of Cape Town | Yes | No | No | No |
| *Equus zebra zebra* | 14/38 | (MODERN) | Left | Upper | University of Cape Town | Yes | Yes | No | No |
| *Equus caballus* | 11/20 | (MODERN) | Right | Upper | University of Cape Town | Yes | No | No | No |
| *Equus quagga* | 13/198 | (MODERN) | Right | Upper | University of Cape Town | Yes | Yes | No | No |
| *Equus capensis* | GV7598 | GLADYSVALE | Right | Upper | University of the Witswaterstrand | No | Yes | No | Yes |
| *Equus capensis* | GVD1-220 | GLADYSVALE | Right | Upper | University of the Witswaterstrand | No | Yes | No | Yes |
| *Equus capensis* | GV391-B133 | GLADYSVALE | Right | Upper | University of the Witswaterstrand | Yes | Yes | Yes | Yes |
| *Equus capensis* | GV402 | GLADYSVALE | Right | Upper | University of the Witswaterstrand | No | Yes | No | Yes |
| *Equus quagga* | PL5854 | PLOVERS LAKE | Left | Upper | University of the Witswaterstrand | No | Yes | No | Yes |
| *Equus quagga* | PL17743 | PLOVERS LAKE | Right | Upper | University of the Witswaterstrand | No | Yes | Yes | Yes |
| *Equus quagga* | PV17790 | PLOVERS LAKE | Left | Upper | University of the Witswaterstrand | Yes | Yes | Yes | Yes |
| *Equus capensis* | 28881 | SWARTKRANS | Right | Upper | University of the Witswaterstrand | No | Yes | No | Yes |
| *Equus capensis* | COH160 | MAKAPANSGAT | Right | Upper | University of the Witswaterstrand | Yes | Yes | Yes | Yes |
| *Equus capensis* | COH127 | MAKAPANSGAT | Right | Upper | University of the Witswaterstrand | No | Yes | No | Yes |
| *Equus capensis* | COH167 | MAKAPANSGAT | Left | Upper | University of the Witswaterstrand | Yes | Yes | Yes | Yes |
| *Equus capensis* | COH69 | MAKAPANSGAT | Right | Upper | University of the Witswaterstrand | Yes | Yes | Yes | Yes |
| *Equus capensis* | COH163 | MAKAPANSGAT | Right | Upper | University of the Witswaterstrand | Yes | Yes | Yes | Yes |
| *Equus capensis* | KB566 | KALKBANK | Left | Upper | University of the Witswaterstrand | Yes | Yes | Yes | Yes |

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|---|---|---|---|---|---|---|---|---|---|
| *Equus capensis* | KB561 | KALKBANK | Left | Upper | University of the Witswaterstrand | Yes | Yes | Yes | Yes |
| *Equus* | KB687 | KALKBANK | Right | Upper | University of the Witswaterstrand | Yes | No | No | No |
| *Equus* | KB563 | KALKBANK | Left | Upper | University of the Witswaterstrand | Yes | No | No | No |
| *Equus* | 330 | KALKBANK | Right | Upper | University of the Witswaterstrand | Yes | No | No | No |
| *Equus* | 325 | KALKBANK | Right | Upper | University of the Witswaterstrand | Yes | No | No | No |
| *Equus quagga* | 323 | KALKBANK | Right | Upper | University of the Witswaterstrand | Yes | Yes | Yes | Yes |
| *Equus capensis* | KB583 | KALKBANK | Left | Upper | University of the Witswaterstrand | No | Yes | No | Yes |
| *Equus capensis* | KB580 | KALKBANK | Left | Upper | University of the Witswaterstrand | Yes | Yes | Yes | Yes |
| *Equus capensis* | KB45 | KALKBANK | Left | Upper | University of the Witswaterstrand | No | Yes | Yes | Yes |
| *Equus capensis* | KB579 | KALKBANK | Left | Upper | University of the Witswaterstrand | Yes | Yes | No | Yes |
| *Equus capensis* | KB581 | KALKBANK | Right | Upper | University of the Witswaterstrand | No | Yes | No | Yes |
| *Equus capensis* | KB1565 | KALKBANK | Right | Upper | University of the Witswaterstrand | Yes | Yes | Yes | Yes |
| *Equus capensis* | KB567 | KALKBANK | Right | Upper | University of the Witswaterstrand | Yes | Yes | Yes | Yes |
| *Equus capensis* | KB45 | KALKBANK | Left | Upper | University of the Witswaterstrand | Yes | Yes | Yes | Yes |
| *Equus capensis* | KB572 | KALKBANK | Right | Upper | University of the Witswaterstrand | Yes | Yes | Yes | Yes |
| *Equus quagga* | 130 | KALKBANK | Right | Upper | University of the Witswaterstrand | Yes | Yes | Yes | No |
| *Equus* | 324 | KALKBANK | Left | Upper | University of the Witswaterstrand | Yes | No | No | No |
| *Equus capensis* | 390 | KALKBANK | Left | Upper | University of the Witswaterstrand | No | Yes | No | Yes |
| *Equus capensis* | 392 | KALKBANK | Right | Upper | University of the Witswaterstrand | Yes | Yes | Yes | Yes |
| *Equus quagga* | KB653 | KALKBANK | Right | Upper | University of the Witswaterstrand | Yes | Yes | Yes | Yes |
| *Equus quagga* | KB704 | KALKBANK | Right | Upper | University of the Witswaterstrand | No | Yes | No | Yes |
| *Equus quagga* | KB676 | KALKBANK | Right | Upper | University of the Witswaterstrand | No | Yes | No | Yes |
| *Equus quagga* | KB702 | KALKBANK | Right | Upper | University of the Witswaterstrand | Yes | Yes | Yes | Yes |
| *Equus quagga* | KB680 | KALKBANK | Right | Upper | University of the Witswaterstrand | Yes | Yes | Yes | Yes |
| *Equus quagga* | KB677 | KALKBANK | Right | Upper | University of the Witswaterstrand | Yes | Yes | Yes | Yes |
| *Equus quagga* | KB685 | KALKBANK | Right | Upper | University of the Witswaterstrand | Yes | Yes | Yes | Yes |
| *Equus quagga* | KB700 | KALKBANK | Right | Upper | University of the Witswaterstrand | Yes | Yes | Yes | Yes |

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|---|---|---|---|---|---|---|---|---|---|
| *Equus quagga* | KB654 | KALKBANK | Left | Upper | University of the Witswaterstrand | Yes | Yes | Yes | Yes |
| *Equus quagga* | KB691 | KALKBANK | Left | Upper | University of the Witswaterstrand | Yes | Yes | Yes | Yes |
| *Equus quagga* | KB655 | KALKBANK | Left | Upper | University of the Witswaterstrand | Yes | Yes | Yes | Yes |
| *Equus quagga* | KB705 | KALKBANK | Left | Upper | University of the Witswaterstrand | No | Yes | No | Yes |
| *Equus quagga* | KB659 | KALKBANK | Left | Upper | University of the Witswaterstrand | Yes | Yes | Yes | Yes |
| *Equus quagga* | KB692 | KALKBANK | Left | Upper | University of the Witswaterstrand | Yes | Yes | Yes | Yes |
| *Equus quagga* | KB695 | KALKBANK | Left | Upper | University of the Witswaterstrand | Yes | Yes | Yes | Yes |
| *Equus quagga* | KB679 | KALKBANK | Left | Upper | University of the Witswaterstrand | Yes | Yes | Yes | Yes |
| *Equus quagga* | KB672 | KALKBANK | Left | Upper | University of the Witswaterstrand | Yes | Yes | Yes | Yes |
| *Equus quagga* | 328 | KALKBANK | Left | Upper | University of the Witswaterstrand | Yes | Yes | Yes | Yes |
| *Equus quagga* | 359 | KALKBANK | Left | Upper | University of the Witswaterstrand | Yes | Yes | Yes | Yes |
| *Equus capensis* | CD5881 | COOPERS CAVE | Right | Upper | University of the Witswaterstrand | Yes | Yes | Yes | Yes |
| *Equus capensis* | CD9293 | COOPERS CAVE | Right | Upper | University of the Witswaterstrand | No | Yes | No | Yes |
| *Equus quagga/capensis* | COH68 | SWALLOW HOLE | Left | Upper | University of the Witswaterstrand | Yes | Yes | No | Yes |
| *Equus quagga/capensis* | COH170 | SWALLOW HOLE | Right | Upper | University of the Witswaterstrand | Yes | Yes | No | Yes |
| *Equus quagga/capensis* | COH161 | SWALLOW HOLE | Right | Upper | University of the Witswaterstrand | Yes | Yes | No | Yes |
| *Equus quagga/capensis* | COH276 | SWALLOW HOLE | Right | Upper | University of the Witswaterstrand | Yes | Yes | No | Yes |
| *Equus quagga/capensis* | COH227 | SWALLOW HOLE | Right | Upper | University of the Witswaterstrand | Yes | Yes | No | Yes |
| *Equus quagga/capensis* | COH169 | SWALLOW HOLE | Right | Upper | University of the Witswaterstrand | Yes | Yes | No | Yes |
| *Equus quagga/capensis* | COH360 | SWALLOW HOLE | Right | Upper | University of the Witswaterstrand | No | Yes | No | Yes |
| *Equus quagga/capensis* | COH164 | SWALLOW HOLE | Right | Upper | University of the Witswaterstrand | Yes | Yes | No | Yes |
| *Equus quagga/capensis* | COH188 | SWALLOW HOLE | Left | Upper | University of the Witswaterstrand | Yes | Yes | No | Yes |
| *Equus quagga/capensis* | COH136 | SWALLOW HOLE | Left | Upper | University of the Witswaterstrand | Yes | Yes | No | Yes |
| *Equus quagga/capensis* | COH28 | SWALLOW HOLE | Right | Upper | University of the Witswaterstrand | No | Yes | No | Yes |
| *Equus quagga/capensis* | COH155 | SWALLOW HOLE | Left | Upper | University of the Witswaterstrand | Yes | Yes | No | Yes |
| *Equus quagga/capensis* | N/A | SWALLOW HOLE | Left | Upper | University of the Witswaterstrand | Yes | Yes | No | Yes |
| *Equus quagga* | COH21-24 | SWALLOW HOLE | Right | Upper | University of the Witswaterstrand | Yes | Yes | Yes | Yes |

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|---|---|---|---|---|---|---|---|---|---|
| *Equus quagga* | COH15-19 | SWALLOW HOLE | Left | Upper | University of the Witswaterstrand | Yes | Yes | Yes | Yes |
| *Equus quagga/capensis* | COH3 | SWALLOW HOLE | Right | Upper | University of the Witswaterstrand | Yes | Yes | No | Yes |
| *Equus quagga/capensis* | COH134 | SWALLOW HOLE | Right | Upper | University of the Witswaterstrand | No | Yes | No | Yes |
| *Equus quagga/capensis* | COH173 | SWALLOW HOLE | Right | Upper | University of the Witswaterstrand | Yes | Yes | No | Yes |
| *Equus quagga/capensis* | COH370 | SWALLOW HOLE | Left | Upper | University of the Witswaterstrand | No | Yes | No | Yes |
| *Equus capensis* | COH10 | CAVE OF HEARTHS | Left | Upper | University of the Witswaterstrand | Yes | Yes | Yes | Yes |
| *Equus capensis* | COH53 | CAVE OF HEARTHS | Right | Upper | University of the Witswaterstrand | No | Yes | No | Yes |
| *Equus capensis* | COH59 | CAVE OF HEARTHS | Right | Upper | University of the Witswaterstrand | Yes | Yes | No | Yes |
| *Equus quagga* | COH27 | CAVE OF HEARTHS | Left | Upper | University of the Witswaterstrand | No | Yes | No | Yes |
| *Equus quagga* | COH54 | CAVE OF HEARTHS | Left | Upper | University of the Witswaterstrand | No | Yes | No | Yes |
| *Equus quagga* | COH5 | CAVE OF HEARTHS | Left | Upper | University of the Witswaterstrand | No | Yes | No | Yes |
| *Equus quagga* | COH18 | CAVE OF HEARTHS | Right | Upper | University of the Witswaterstrand | Yes | Yes | Yes | Yes |
| *Equus quagga* | COH44 | CAVE OF HEARTHS | Right | Upper | University of the Witswaterstrand | Yes | Yes | Yes | Yes |
| *Equus quagga* | 19HO | CAVE OF HEARTHS | Left | Upper | University of the Witswaterstrand | Yes | Yes | Yes | Yes |
| *Equus quagga* | COH245 | CAVE OF HEARTHS | Right | Upper | University of the Witswaterstrand | Yes | Yes | Yes | Yes |
| *Equus quagga* | COH165 | CAVE OF HEARTHS | Right | Upper | University of the Witswaterstrand | No | Yes | No | Yes |
| *Equus quagga* | COH111 | CAVE OF HEARTHS | Right | Upper | University of the Witswaterstrand | No | No | No | Yes |
| *Equus quagga* | COH111 | CAVE OF HEARTHS | Right | Upper | University of the Witswaterstrand | Yes | Yes | Yes | Yes |
| *Equus quagga* | COH130 | CAVE OF HEARTHS | Right | Upper | University of the Witswaterstrand | No | Yes | No | Yes |
| *Equus quagga* | COH141 | CAVE OF HEARTHS | Right | Upper | University of the Witswaterstrand | Yes | Yes | Yes | Yes |
| *Equus* | COH21 | BUFFALO CAVE | Right | Upper | University of the Witswaterstrand | Yes | No | No | No |
| *Equus quagga* | COH594 | CAVE OF HEARTHS | Right | Upper | University of the Witswaterstrand | No | Yes | No | Yes |
| *Equus* | C2039 | MAHEMSPAN | Right | Upper | University of the Witswaterstrand | Yes | No | No | No |
| *Equus* | C2124 | MAHEMSPAN | Left | Upper | University of the Witswaterstrand | Yes | No | No | No |
| *Equus* | C2061 | MAHEMSPAN | Right | Upper | University of the Witswaterstrand | Yes | No | No | No |
| *Equus* | C2558 | MAHEMSPAN | Right | Upper | University of the Witswaterstrand | Yes | No | No | No |
| *Equus* | C2115 | MAHEMSPAN | Right | Upper | University of the Witswaterstrand | Yes | No | No | No |

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|---|---|---|---|---|---|---|---|---|---|
| *Equus* | C2560 | MAHEMSPAN | Left | Upper | University of the Witswaterstrand | Yes | No | No | No |
| *Equus* | C2126 | MAHEMSPAN | Left | Upper | University of the Witswaterstrand | Yes | No | No | No |
| *Equus* | C2560 | MAHEMSPAN | Left | Upper | University of the Witswaterstrand | Yes | No | No | No |
| *Equus* | C1374 | MAHEMSPAN | Right | Upper | University of the Witswaterstrand | Yes | No | No | No |
| *Equus* | C2124 | MAHEMSPAN | Left | Upper | University of the Witswaterstrand | Yes | No | No | No |
| *Equus* | 26-323 | EQUUS CAVE | Left | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | EC1042 | EQUUS CAVE | Right | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | EC1039 | EQUUS CAVE | Right | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | EC1041 | EQUUS CAVE | Left | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | EC1045 | EQUUS CAVE | Right | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | EC1044 | EQUUS CAVE | Left | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | EC1040 | EQUUS CAVE | Right | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | J19 27-29 | EQUUS CAVE | Right | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | EC1037 | EQUUS CAVE | Left | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | EC1068 | EQUUS CAVE | Right | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | EC108 | EQUUS CAVE | Left | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | EC1082 | EQUUS CAVE | Right | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | EC1083 | EQUUS CAVE | Right | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | EC1076 | EQUUS CAVE | Right | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | EC1084 | EQUUS CAVE | Left | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |

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|---|---|---|---|---|---|---|---|---|---|
| *Equus* | EC902 | EQUUS CAVE | Left | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | EC1149 | EQUUS CAVE | Left | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | EC1157 | EQUUS CAVE | Right | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | EC961 | EQUUS CAVE | Left | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | EC1112 | EQUUS CAVE | Right | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | EC1026 | EQUUS CAVE | Left | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | EC147 | EQUUS CAVE | Left | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | EC1111 | EQUUS CAVE | Left | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | EC345 | EQUUS CAVE | Right | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | EC298 | EQUUS CAVE | Left | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | EC1127 | EQUUS CAVE | Right | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | EC458 | EQUUS CAVE | Left | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | EC1024 | EQUUS CAVE | Left | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | EC286 | EQUUS CAVE | Left | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | EC454 | EQUUS CAVE | Left | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | EC952 | EQUUS CAVE | Left | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | EC1322 | EQUUS CAVE | Right | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | EC340 | EQUUS CAVE | Left | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |

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|---|---|---|---|---|---|---|---|---|---|
| *Equus* | EC456 | EQUUS CAVE | Left | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | EC1600 | EQUUS CAVE | Left | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | EC1610 | EQUUS CAVE | Right | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | EC907 | EQUUS CAVE | Left | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | EC1170 | EQUUS CAVE | Left | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | EC453 | EQUUS CAVE | Left | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | EC1262 | EQUUS CAVE | Left | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | EC1257 | EQUUS CAVE | Left | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | EC1261 | EQUUS CAVE | Right | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | EC1260 | EQUUS CAVE | Left | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | EC993 | EQUUS CAVE | Right | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | EC1169 | EQUUS CAVE | Left | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | EC1259 | EQUUS CAVE | Right | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | EC289 | EQUUS CAVE | Left | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | EC334 | EQUUS CAVE | Right | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | EC1056 | EQUUS CAVE | Left | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | EC373 | EQUUS CAVE | Left | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | EC1197 | EQUUS CAVE | Left | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |

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|---|---|---|---|---|---|---|---|---|---|
| *Equus* | EC1267 | EQUUS CAVE | Right | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | EC190 | EQUUS CAVE | Right | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | EC1080 | EQUUS CAVE | Left | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | EC131 | EQUUS CAVE | Right | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | EC1185 | EQUUS CAVE | Left | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | EC904 | EQUUS CAVE | Right | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | EC1174 | EQUUS CAVE | Right | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | EC330 | EQUUS CAVE | Right | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | EC1087 | EQUUS CAVE | Right | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | EC1148 | EQUUS CAVE | Right | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | EC955 | EQUUS CAVE | Left | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | EC335 | EQUUS CAVE | Left | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus capensis* | PKA218 | SPITSKOP | Right | Upper | Florisbad Quaternary Research Station | Yes | Yes | Yes | Yes |
| *Equus capensis* | PKA216 | SPITSKOP | Left | Upper | Florisbad Quaternary Research Station | No | Yes | No | Yes |
| *Equus capensis* | PKA211 | SPITSKOP | Right | Upper | Florisbad Quaternary Research Station | Yes | Yes | Yes | Yes |
| *Equus capensis* | PKA222 | SPITSKOP | Right | Upper | Florisbad Quaternary Research Station | Yes | Yes | Yes | Yes |
| *Equus capensis* | PKA213 | SPITSKOP | Left | Upper | Florisbad Quaternary Research Station | No | Yes | No | Yes |
| *Equus capensis* | PKA217 | SPITSKOP | Right | Upper | Florisbad Quaternary Research Station | No | Yes | No | Yes |

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|---|---|---|---|---|---|---|---|---|---|
| *Equus capensis* | PKA220 | SPITSKOP | Right | Upper | Florisbad Quaternary Research Station | Yes | Yes | Yes | Yes |
| *Equus capensis* | PKA221 | SPITSKOP | Left | Upper | Florisbad Quaternary Research Station | No | Yes | No | Yes |
| *Equus* | FLO2778 C1521 | FLORISBAD | Left | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | FLO2596 C1521 | FLORISBAD | Left | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | FLO2638 C1521 | FLORISBAD | Left | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | FLO2546 C1521 | FLORISBAD | Left | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | FLO2619 C2784 | FLORISBAD | Left | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | FLO2617 C1477 | FLORISBAD | Left | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | FLO2560 | FLORISBAD | Left | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | FLO6061 C1524 | FLORISBAD | Right | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | FLO6060 C1521 | FLORISBAD | Right | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | FLO6058 C1521 | FLORISBAD | Left | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | FLO4878 | FLORISBAD | Right | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | FLO1728 C1521 | FLORISBAD | Right | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | FLO2767 C1521 | FLORISBAD | Left | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | FLO2764 C2921 | FLORISBAD | Left | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | FLO2671 C1521 | FLORISBAD | Left | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | FLO1726 C1521 | FLORISBAD | Right | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |

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|---|---|---|---|---|---|---|---|---|---|
| *Equus* | FLO6050 C1521 | FLORISBAD | Right | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | FLO6047 C1521 | FLORISBAD | Right | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | FLO2769 C1521 | FLORISBAD | Left | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | FLO2517 C1521 | FLORISBAD | Right | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | FLO2783 C1521 | FLORISBAD | Right | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | VLA116 | VLAKRAAL | Right | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | VLA123 | VLAKRAAL | Right | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | VLA120 | VLAKRAAL | Right | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | VLA115 | VLAKRAAL | Right | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | VLA122 | VLAKRAAL | Right | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | VLA3 C1521 | VLAKRAAL | Left | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | VLA67 C1521 | VLAKRAAL | Left | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | VLA12 C1521 | VLAKRAAL | Right | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | VLA2 C1521 | VLAKRAAL | Left | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | VLA65 C1521 | VLAKRAAL | Right | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | VLA1 C1521 | VLAKRAAL | Left | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | VLA118 | VLAKRAAL | Right | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | VLA8 C1521 | VLAKRAAL | Left | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |

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|---|---|---|---|---|---|---|---|---|---|
| *Equus* | VLA68 C1521 | VLAKRAAL | Left | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | VLA59 C1521 | VLAKRAAL | Left | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | VLA6 C1521 | VLAKRAAL | Left | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | VLA117 | VLAKRAAL | Left | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | VLA17 | VLAKRAAL | Left | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | VLA16 C1521 | VLAKRAAL | Right | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | VLA11 C1521 | VLAKRAAL | Right | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | VLA128 | VLAKRAAL | Right | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | VLA124 | VLAKRAAL | Left | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | VLA113 | VLAKRAAL | Right | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | SR52 | SAND RIVER | Right | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus* | SRK32 | SAND RIVER | Right | Upper | Florisbad Quaternary Research Station | Yes | No | No | No |
| *Equus quagga* | SAM-AA B6 YSL | NELSON BAY CAVE | Left | Upper | Iziko South African museum | Yes | Yes | No | Yes |
| *Equus quagga* | SAM-AA D4 YSL | NELSON BAY CAVE | Left | Upper | Iziko South African museum | No | Yes | No | Yes |
| *Equus oldowayensis* | KNM-OG 22833 | EASTERN RIFT VALLEY | Left | Upper | National Museums of Kenya | Yes | Yes | No | No |
| *Equus* aff. *capensis* | 5016 | OLORGESAILIE | Left | Upper | National Museums of Kenya | No | Yes | No | No |
| *Equus* aff. *capensis* | 1019 | OLORGESAILIE | Right | Upper | National Museums of Kenya | Yes | Yes | No | No |
| *Equus* aff. *capensis* | 4939 | OLORGESAILIE | Right | Upper | National Museums of Kenya | Yes | Yes | No | No |
| *Equus grevyi* | KNM-AB 24280 | AMBOSELI | Right | Upper | National Museums of Kenya | Yes | Yes | No | No |